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LARVAL DEVELOPMENT OF THE POLYCHAETE FAMILIES SPIONIDAE SARS, DISOMIDAE MESNIL, AND POECILOCHAETIDAE N. FAM. IN THE GULLMAR FJORD (SWEDEN)

BY

LENNART HANNERZ

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FIL. LIC., VÄRML.

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LENNART HANNERZ

(Royal Fishery Board of Sweden, Göteborg)

With 57 figures in the text

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The work was begun at Klubbans Biologiska Station, Fiskebäckskil, in the summer of 1947 and continued there during the summer months of 1948–50. During this period I received valuable assistance from Dr. B. FORSMAN who helped me over the difficulties in the beginning, gave me much good advice and placed valuable notes at my disposal. I should also like to thank him for his continued interest in my work.

From January 1951, when I became an assistant at Kristinebergs Zoologiska Station, Fiskebäckskil, I have been able to pursue my studies all the year round. I am greatly indebted to the former head of the station, the late Prof. NILS HOLMGREN, Stockholm, and its director, Dr. G. GUSTAFSON, for their kindness in permitting me to use so great a part of my office time for my own research. I should like to thank Dr. GUSTAFSON also for giving me the advantage of his many years' experience of the fauna of the Gullmar Fjord. Numerous local data on the species treated in this study have emanated from him.

For fruitful discussions, advice, and encouragement I should also like to thank Dr. LARS SILÉN, Stockholm. My gratitude is likewise due to many others, all of whom cannot be mentioned here, for their interest and good advice.

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Last but not least, I should like to thank the staff of Kristinebergs Zoological Station for their aid in collecting material.

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Introduction

Since the pioneer work of Lovén (1842), "Iakttagelse öfver metamorfosen hos en annelid", the investigation of the development of polychaets attracted the interest of a great many scientists. Even earlier, however, Martinus Slabber (1778) had reproduced the first polychaet larva known in literature, without realizing its character of a larva.

Since then an extensive literature has appeared in this field. The pelagic larvae of the *Spionidae*, which constitute the largest and most beautiful in plankton and, moreover, often are the most numerous, naturally were described, at an early date.

Örsted (1843) with the description of "*Pullus Leucodori ciliatii*" was the first to give an account of a Spionid larva which was specifically determined. Important works describing larvae of the families treated in the present paper have thereafter been published by Frey and Leuckart (1847), Bush (1851), Leuckart (1855), Leuckart and Pagenstecher (1858), Claparède (1863), Agassiz (1867), Claparède and Mecznikow (1869), Fewkes (1883), v. Drasche (1885), Cunningham and Ramage (1888), Mesnil (1896), and others. The morphology and histology of the Spionid larvae were treated in greater detail by Häcker (1896). Salensky (1908) studied the mouth region of the Spionid larvae and Gravely (1909) published two papers dealing with their ciliation and formation of the mouth region and endeavored, moreover, to arrange them in a larval system. Among others who have studied larvae of the families concerned in this paper may also be mentioned Leschke (1903), Cerruti (1911), Mesnil (1916), Mesnil and Caullery (1917), Caullery and Mesnil (1918), Hofker (1920, 1930), and Flattely (1923). Söderström (1920) in a monograph on the *Spionidae* described interesting features in the biology of reproduction among some species and proposed among other things a theory for the formation of the so-called egg-capsules in the brood-protecting species. D. P. Wilson, who has carried out a series of outstanding investigations on larval development and biology in several polychaete species, has treated in one paper also the development in a couple of *Polydora* species (1928). An excellent study concerning the entire development of *Scolelepis fuliginosa* has been made by Day (1934). Finally, the development of the Spionidae and their larval forms have been treated in larger connections by Thorson (1946) and Smidt (1951).

From this literature we have acquired a rather detailed knowledge of

the morphology of these larvae and, to a certain extent, also their biology. However the descriptions have for the most part been made at random and the biological observations have been more or less accidental. In many cases, perhaps the vast majority, the species of the larvae could not be ascertained, and they have been given provisional names. Regarding the identity of a species speculations have frequently been made which have often led to false conclusions.

That earlier works up to the present time give a relatively incomplete knowledge of the larval development in the families treated can be verified by the fact that in so modern an investigation as THORSON's (1946) 7 Spionid larvae encountered could not be identified as to species or genus.

The aim of the present investigation has been to give an account of the larval development in the *Spionidae*, the *Disomidae*, and the *Poecilochaetidae* for the species which occur in the area of investigation. Furthermore, the intention has been to make a contribution to the understanding of the systematic arrangement of the families concerned. In addition I have attempted to construct an identification table whereby the identity of the planktonic larva can be ascertained.

Material and Methods

Since the aim of this investigation has been to study the entire development of the species concerned, sexually mature animals have been brought to the laboratory where they were kept in cultures. On a few occasions it has been possible to obtain larvae in this manner. Some experiments with artificial fertilization have been performed but with limited success.

The material I have mainly worked with consisted, however, of larvae obtained from plankton. Plankton nets of different sizes and construction, fitted with filtering cloth of varying coarseness, mostly so-called "Müller-gauze", nos. 6, 8, and 12 with mesh widths of 348 μ, 294 μ, and 202 μ respectively, have been employed and both horizontal and vertical netting have been carried out. In the horizontal netting the depth varied from 0 to about 100 meters. For the vertical netting I have made use of one and the same net with a ring diameter of about 1.5 metre and fitted with "Müller-gauze" no. 8, which has been drawn in one and the same place from a depth of 50 metres up to the surface. After carefully mixing the sample thus obtained, 100 ml thereof were examined and the number of larvae of different species counted; thereafter the total volume of the sample was measured. Thus the total number of larvae in the sample could be approximately calculated. In this manner the density of the larvae from different periods could be compared (see p. 182).

The larvae of the different species have been sorted out in bowls with

sea-water containing 15 or 40 ml. If not too many larvae are placed together in such bowls, they can survive for remarkably long time, especially if the water be occasionally changed.

The bowls have been stored on an aquarium table with running water. Where it was necessary to keep the water in the bowls in constant circulation an apparatus especially constructed for this purpose (HANNERZ 1953) has been employed.

Representative larvae have been studied and drawn under the microscope. I have made a point of drawing all pictures from living specimens. In this work it has been impossible to use a camera lucida, as the larvae are constantly in rapid motion. Instead the method with square ruled paper and a squared-net micrometer in the eye-piece, which has been described by WILSON (1928), has been employed. Since the larvae are exceedingly mobile it has been quite too tedious and laborious to study them without lightly squeezing them between slide and cover-glass. In my drawings I have endeavoured to correct the changes in body form which have resulted from this procedure.

In order to connect the larvae with their respective benthonic stages the larvae have been cultured via metamorphosis to such a stage that identification of the species has been possible. It has been shown that the metamorphosis was to a greater or lesser degree dependent on a specific substratum, which is in accordance with the findings that have been made with other pelagic larvae. In certain cases it has been impossible to get the larvae to metamorphose.

The culture bowls have been filled to about $^2/_3$ with water and provided with a thin layer of bottom substratum. As nutriment for the benthonic stages principally cultures of *Nitzschia closterium* but also planktonic organisms have been used. The algal cultures have been grown in a culture medium according to GROSS (1937) and later in a modification thereof according to BAINBRIDGE (1953).

At suitable times after the metamorphosis cultures of young benthonic stages have been examined and these have been saved, studied, and figured in the same manner as the pelagic larvae.

During the course of the investigation both pelagic larvae and young benthonic stages have been conserved for study in sections or preparations of whole specimens. I have found cocaine to be the best anaesthetic, but magnesium sulphate has also been used. The fixation has been made with BOUIN's fixation fluid heated to about 60–70°C, in which the anaesthetized individuals were placed by means of a pipette. The method which was recommended by DALES (1950) for *Nereis* larvae was found to be excellent even here, as it was important to have the larvae fixed in an outstretched condition.

I. DESCRIPTIVE PART

Identification Key for Pelagic Larvae

For the reasons of surveyability I prefer to include here only larvae that are ready to metamorphose. This refers also to the identification keys which are to be found together with the descriptions of the respective genera.

Spionidae Sars, *Disomidae* Mesnil and *Poecilochaetidae* n. fam.

The larva is extended and as a rule gets a relatively large number of segments. Posteriorly directed, long, finely serrated larval setae are encountered (they are shed in older individuals of some species). The ciliation is composed mainly of proto- and telotroch as well as of intervening gastro- and nototrochs. (The last mentioned is completely lacking in a number of species.) A neurotroch is usually found. It is very short and never extends farther caudad than up to and including segment 2. Posteriorly it ends, with a few exceptions, in a "ciliated pit" (p. 161).

1. Prostomium and peristomium are fused into a large, relatively outspred shield. fam. *Disomidae* (p. 140).
   Prostomium and peristomium not fused in this manner. 2.
2. The larvae become very big (up to 50 segments). The pigmentation is slight. Only lateral chromatophores occurring in each segment are obvious (light green in reflected light). The larval setae are relatively weak. These and the larval ciliation are not found in older pelagic larvae. fam. *Poecilochaetidae* (p. 136).
   Larvae of fair size (maximum 30 segments). Larval setae and ciliation are as a rule not lost. fam. *Spionidae* (p. 8) 3.
3. Complete gastrotrochs are found *in all* segments caudad to the "ciliated pit". There are two pairs of simple red (exception *Prionospio malmgreni*) eyes. The pigmentation is often weak. The body form is extremely variable. The prostomium is for the most part well demarcated from the peristomium. 4.
   Gastrotrochs are *not* found *in all* segments caudad to a "ciliated pit". There are three pairs of black eyes. The most lateral are compound. 8.
4. Parts of the prostomium and peristomium are anteriorly drawn out into a tip. g. *Nerine* and g. *Nerinides* (p. 8).
   The prostomium is more or less stumpy. 5.
5. Long, very thin larvae. The peristomium is less well defined. The pigmentation is slight. g. *Prionospio* (p. 40).
   Small and medium-sized species, not as thin as the foregoing. 6.
6. The body is not transparent due to abundance of yolk; in reflected light it is yellowish white. The larval setae are long and straight. Small larvae. g. *Aonides* (p. 26).
   The body is not rich in yolk. 7.
7. The larval setae are flattened, unilaterally serrated, and occur in both noto- and neuropodia. Small larvae. g. *Laonice* (p. 22).

The larval setae are not flattened and occur only in the notopodia. In segment 1 there is an adult, curved bristle. Medium-sized larvae. One of the species with lateral prostomial processes. g. *Spiophanes* (p. 32).

8. The prostomium is well demarcated from the peristomium. The palpi are attached relatively laterally. Small larvae (maximum 12–13 segments). The parapodia are differentiated to a high degree. The nototrochs are weakly developed. g. *Scolelepis* (p. 52).

   The peristomium is not well demarcated from the prostomium. Palpi are attached relatively more medially. The nototrochs are well developed. 9.

9. The gastrotrochs occur regularly in every other segment caudad to the "ciliated pit". 10.

   Gastrotrochs are not regularly arranged. A "ciliated pit" is usually lacking. Permanent, specialized bristles appear in segm. 5. g. *Polydora* (p. 100).

   No permanent specialized bristles in segm. 5. Small larvae (maximum 15 segments). g. *Pygospio* (p. 90).

10. The "ciliated pit" is well developed. g. *Spio* and g. *Microspio* (p. 61).

A. *Spionidae* Sars

Nerinides Mesnil and *Nerine* Johnston (sensu Mesnil)

The larval development in these two genera is so similar that I prefer to treat them together.

The egg and sperm. The egg has a thick membrane and "membrane vesicles" (p. 151). The sperm is of the short-headed type.

Type of development. The development is entirely pelagic and predominantly planktotrophic.

The pelagic larva. The prostomium is drawn out into an anteriorly directed tip encasing a muscular process originating from the peristomium. The lateral parts of the peristomium are clearly demarcated from the prostomium. The palpi are developed late and attached far out on the lateral parts of the peristomium. There are two pairs of reddish eyes. The parapodia are as a rule weakly differentiated, and the nototrochs slightly developed or totally lacking. The pygidium is rounded and has occasionally a slight dorsal notch. The telotroch is markedly robust. The larval setae are relatively short, strong, and somewhat curved. A "ciliated pit" is found in segment 2. Gastrotrochs occur in all segments from nos. 2–3.

Key to species:

1. The intestinal canal is coloured green and brown. 2.

   The intestinal canal is not coloured in this manner. 3.

2. The "pharynx" is pigmented orange, Long and slender larvae. *Nerine cirratulus* (p. 16).

   No orange pigment in the "pharynx". Short and stumpy larva. Large pygidium. *Nerine sp.* I. (p. 18).

3. The pharynx is distinctly pigmented black. Orange pigment (reflected light) occurs laterally in the anterior segments. The prototroch is divided into two contiguous sections. *Nerinides tridentata* (p. 9).
The pharynx is not distinctly pigmented black. No orange pigment laterally. The prototroch is not divided into two contiguous sections. Often diffuse pigmentation. 4.
4. Lateral, dorsal, red pigment spots in the segments. Large, curved bristles (fig. 5 b) in the posterior segments. *Nerine sp. II.* (p. 20).
No dorsal, red pigment spots. No large, curved bristles in the posterior segments. *Nerine foliosa* (p. 11).

Nerinides tridentata Southern

Occurrence in the area of investigation

This species is known from several localities within the area of investigation (Molander 1930). I myself have obtained it on mud bottom (depth = c. 40 m) outside of Röbergsskären in the Gullmar Fjord.

Occurrence in plankton

Larvae have been obtained in plankton from the beginning of July to the beginning of November.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
6	0.54	0.22
10	0.70	0.28
13	0.88	0.32
15	1.02	0.32
19	1.20	0.38

The larva agrees in type with that of *Nerine foliosa*. It is relatively difficult to distinguish the two at a glance. It is, however, characterized by its very distinctly pigmented pharynx, by the fact that the prototroch is clearly divided into two contiguous sections, by the orange pigment laterally in the anterior segments of older larvae, and in later stages by its ventral triserrated hooded crochets of characteristic type.

The larvae ready to metamorphose (fig. 1)

The description is based primarly on a specimen with 19 segments and one with 15 segments.

There are two pairs of tactile cilia laterally on the prostomium. The brownish red eyes are located in an approximately straight line. The proto-

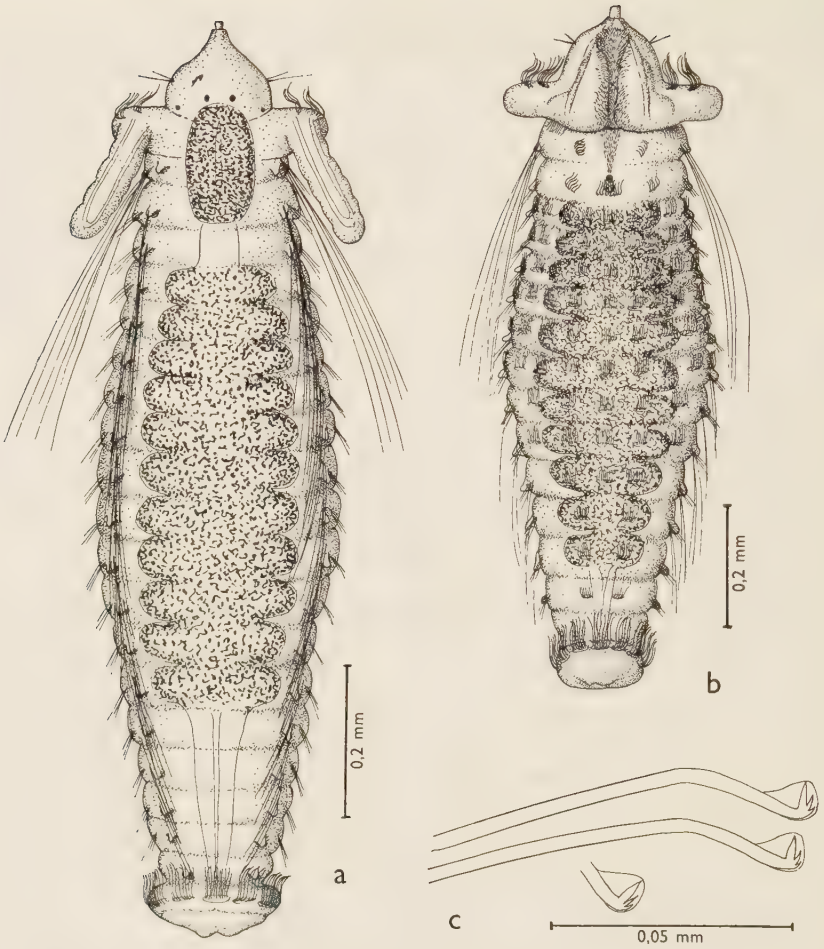


Fig. 1. *Nerinides tridentata* Southern. Pelagic larvae. a) Larva ready to metamorphose (dorsal view). b) Somewhat younger larva (ventral view). c) Ventral crochets from the larva in a.

troch is divided into two contiguous parts. In the parapodia there is a suggestion of dorsal cirri. Branchial anlages are lacking. The posterior part of the back shows a diffuse dark pigmentation. On the inside of the vestibule an orange pigment is often found. The pharynx is distinctly pigmented black (exceptionally brownish yellow), and extends posteriorly up to and including segment 2. Thereafter follows an oesophagus, which is only one segment long. The stomach is yellowish brown to black and has lateral segmental diverticula. The rectum is straight and unpigmented. The anterior part of the neurotroch is surrounded by a pair of large ciliated cells which are located directly posterior to the peristomium and, somewhat farther caudad, by another pair of large ciliated cells. The "ciliated pit" (see p. 161),

which is situated in segment 2, is surrounded by a pair of ciliated cells. Gastrotrochs occur in all segments behind the second. The larval setae are short and relatively lustreless in reflected light. In old larvae dorsal and ventral, permanent, hairy bristles are found in all segments, and in the posterior segments there are also ventral hooded crochets of the type encountered in the adult stage (fig. 1c).

Identity of species

In spite of numerous attempts with varying conditions I have been unsuccessful in getting this larva to metamorphose. The agreement in appearance of the hooded crochets found in the larva and the adult *Nerinides tridentata* is, however, so complete, that I consider it most probable that the larva belongs to this species.

Literature

Thorson (1946) has described a larva, which he called "*Spionid A*", agreeing in general type and pigmentation with the one described here. Since he mainly found it in the spring and I in the late summer the identity is however uncertain.

Nerine foliosa (Audouin et Milne-Edwards)

Occurrence in the area of investigation

The species is known from the area of investigation (Söderström 1920).

Occurrence in plankton

I have found larvae of this species from the beginning of January to the end of April. The youngest stages have been observed only during January and February. Spawning therefore probably takes place during the late winter.

Size and general characteristics of the pelagic larva

Stage	Length mm	Width mm
Young trochophore . .	0.40	0.28
2 segments	0.32	0.18
5 ,, ...	0.45	0.18
7 ,, ...	0.74	0.30
15 ,, ...	1.14	0.42

Differences from the *Nerinides* larva are given on page 9.

The trochophore (fig. 2a)

The egg-membrane does not lie close in to the larval body but surrounds it like a capsule. The prototroch is first formed and thereafter the telotroch. The cilia permeate the egg-membrane as the larval setae do later on. An apical tuft is formed. An incipient formation and stretching of the body takes place. Towards the end of the trochophore stage a pair of red eyes is formed. The larva is opaque yellowish white due to its abundant yolk. Diffuse black pigment is beginning to be formed dorsally.

The 2-segment stage (figs. 2b–d)

The prostomium is widened towards the end of the 2-segment stage and becomes stumpy or even develops a curved notch. Another pair of red eyes appears. It lies medially in relation to the first formed pair. Larval setae and seta sacs are formed. The pygidium is widened and becomes slightly bilobate. The body fills the egg-membrane more and more. A vestibule (p. 156) with a fine ciliation is formed. In the anterior part of the vestibule an anlage to the peristomial process now develops (cf. p. 157). The prototroch and telotroch assume their definite appearance. Dorsally diffuse melanin is observed, otherwise the larva is totally unpigmented apart from the eyes. Due to the abundance of yolk it is still opaque yellowish white. The gut has begun to be differentiated. In segment 1 a distinct "pharynx" is formed. It is followed by a darker gut. The vestibule has begun to be ciliated and the neurotroch as well as the "ciliated pit" have been formed.

The 3-segment stage (fig. 2e)

The egg-membrane has now been completely stretched over the larval body and forms its cuticle. The muscular process has extended considerably and reaches ahead of the prostomium, which is also extended terminally and forms the sheath that surrounds the process. This has developed a ciliation at the tip, and changes posteriorly into two muscular bands which run posteriorly on either side of the mouth opening. The peristomium is very clearly demarcated from the prostomium and the boundary lines can be traced over the "head". The lateral parts of the peristomium form a distinct angle with the prostomium. On the dorsal side of the peristomium anlages to the nuchal organs have been formed as a pair of very finely ciliated grooves. The prostomium has developed a number of tactile cilia. A large one of these is observed on either side projecting posteriorly from the lateral parts of the peristomium. The "pharynx" is distinctly formed and the larva has begun to take up food. Gastrotrochs have not yet been formed.

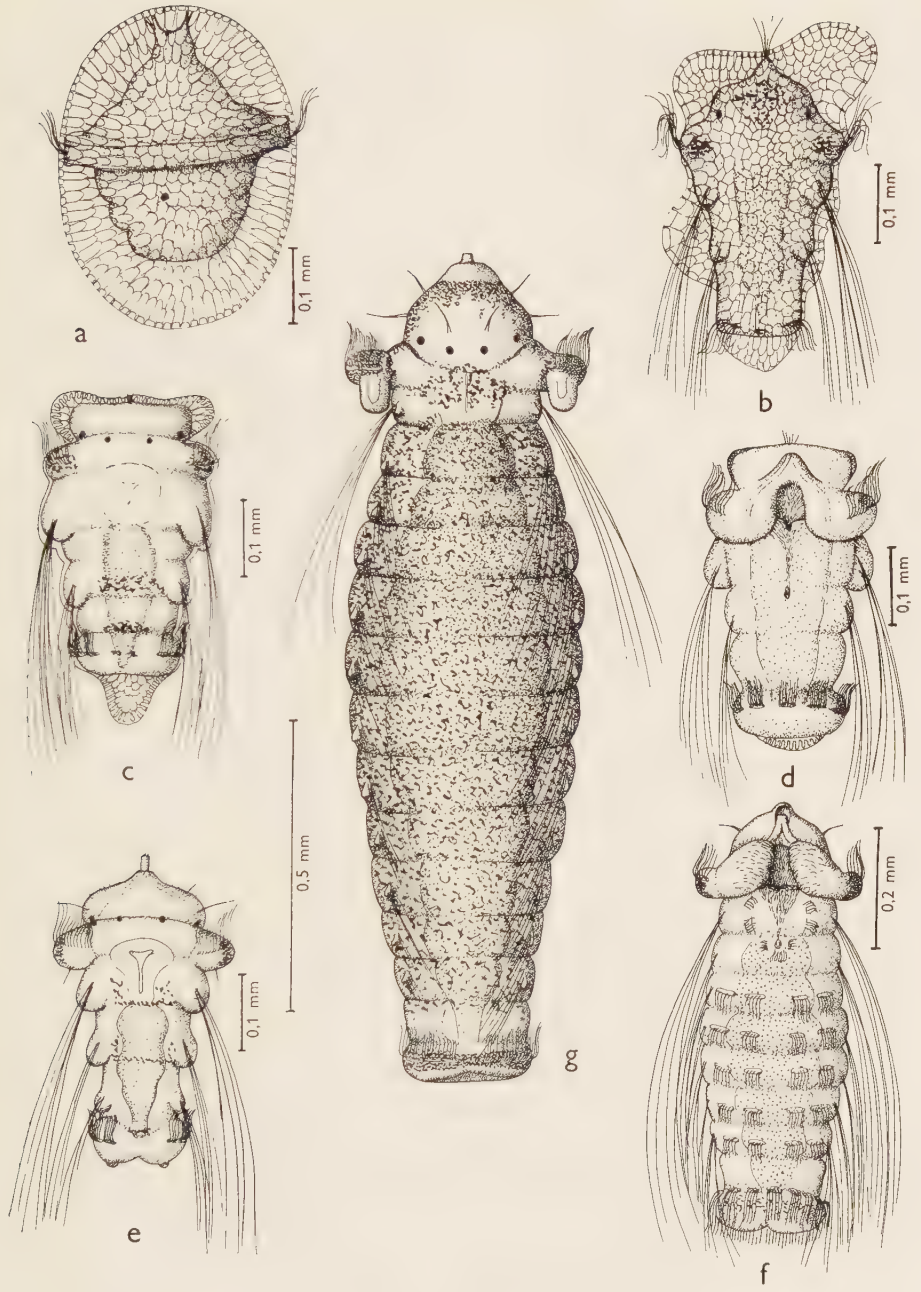


Fig. 2. Pelagic larvae of *Nerine foliosa* (Audouin et Milne Edwards). a) Trochophore. b) Young 2-segment stage. c) Older 2-segment stage (dorsal view). d) Older 2-segment stage (ventral view). e) 3-segment stage (dorsal view). f) 7-segment stage (ventral view). g) Larva ready to metamorphose (dorsal view).

The 7-segment stage (fig. 2f)

Gastrotrochs are now found in all segments beginning with the third. The neurotroch is broadened and in segment 1 it is surrounded by two pairs of ciliated cells. In segment 2 a pair of ciliated cells is found on both sides of the "ciliated pit".

The larva ready to metamorphose (fig. 2g)

In the 15-segment larva the prostomium has not undergone any essential changes. The lateral parts of the peristomium have projected further and now bear a pair of short anlages to palpi, as well as the robustly developed prototroch. Weak dorsal and ventral cirri have been formed in all segments. They decrease in length posteriorly. Branchial anlages are still lacking. Delicate nototrochs occur from segment 2 onwards. The pygidium has developed a dorsal notch. The whole body has assumed a rather dense brownish black pigmentation (not in all individuals). This pigmentation is especially vivid in the posterior part of the body. The lateral parts of the peristomium and the pygidium have taken on a yellowish brown pigmentation. The larval setae are strong, serrated, and somewhat curved. Of the permanent setae there are both dorsal and ventral hairy bristles and from about segment 10 also ventral diserrated hooded crochets. On the inside of the lateral lips a dark brown pigmentation has developed. This pigmentation is also sometimes found in the pharynx. The neurotroch, gastrotrochs, and "ciliated pit" have not undergone any essential changes.

The young benthonic stage

The larva metamorphoses readily in pure mineral sand from localities exposed to waves. Many individuals have been cultured. One specimen could be reared to a length of 19 mm (88 segments). At that time its coelom contained sexual product ($4\frac{1}{2}$ months after metamorphosis).

The palpi develop very quickly. The lateral parts of the peristomium proceed to form toric swellings on the proximal parts of the palpi. These tori gradually disappear. The lower side of the peristomium, especially the ventral lip, grows rapidly and forms a protrusible part. The prostomium retains its tapered form and never becomes trilobate (cf. Fauvel 1927). The eyes remain unchanged. On the most posterior part of the prostomium a small occipital tentacle projects which is well demarcated from the rest of the "head". In all segments there exist dorsal and ventral cirri. As the cirri in the other segments grow rapidly those in segment 1 remain insignificant. The ventral cirri in the anterior part of the body are rounded but have a notch farther caudad in older individuals. The dorsal cirri are first triangular and free from the branchiae in the anterior part of the body,

but as they grow further they will fuse with them. Branchiae are found from the second segment onwards and remain free from the dorsal cirri for their entire length from segment 30–40. Branchiae are formed first relatively late after metamorphosis. Nototrochs are found in all segments from the second onwards. The pygidium increases in size and becomes the rounded knob which is characteristic for this genus. All pigmentation disappears completely. Ventral and dorsal hairy bristles are seen in all segments. In addition there are dorsal and ventral hooded crochets in the posterior part of the body. These bristles are in this stage still diserrated. In the 88-segment individual there were only uniserrated hooded crochets (see p. 170). The ventral bristles of this type occurred from segment 28, and dorsal ones from segment 45 onwards. This individual was epitoquous from 31.

Identity of species

In the specimen with 88 segments mentioned in the foregoing, such adult characteristics had been developed as to preclude confusion with other species. (The fusion of the branchiae with the dorsal cirri in the anterior part of the body and the typical uniserrated hooded crochets.) That the prostomium retains its markedly tapered form until the stage of sexual maturity speaks in favour of the sub-species *Nerine foliosa sarsiana*.

Biology

The bottom stage lives ranging freely in the bottom substratum and does not form any resistant tubes. It is a pronounced predacions. The young specimens which I have reared have eaten young lamellibranch larvae (*Mya*) and gastropod larvae.

Literature

The early development has been studied by Cunningham and Ramage (1888, pp. 635 684, figs. 1d and 1e). They described the fertilized egg and a 4-cell stage. Agassiz (1867) described a larva which he considered as belonging to *Nerine coniocephala* Johnston (syn. *Nerine foliosa* Audouin et Milne-Edwards). His figures and description are, however, so defective that I have been unable to determine whether or not this larva is identical with the one I have described here. Leschke (1903, p. 123, pl. 6, fig. 10) found a trochophore during the winter, which in all probability belongs to this species. Thorson (1946) has been guilty of confounding at least two species in his treatment of the larvae of *Nerine foliosa*. His young trochophores (pp. 79–80, figs. 38 A–G) belong undoubtedly to this species. They agree in size, appearance, and occurrence during the seasons with those I have found. His figures of these young developmental stages are excellent. The larva, which he has described as "*Nectochaeta of medium size*" (p. 81,

fig. 39 A) does not correspond to any of the developmental stages of *Nerine foliosa*. It does not seem to have the generically characteristics "head". Furthermore, it has three pairs of eyes which makes it most likely that it should be placed either in the sub-family *Spioninae* or in the gen. *Scolelepis* (see p. 155). This larva has also been only provisionally classified by THORSON in this species. His "*larva in the oldest planktonic stage known*", which he with hesitation has placed in this species, belongs with all certainty to *Nerine cirratulus*, a possibility also suggested by him.

Nerine cirratulus (Delle-Chiaje)

Occurrence in the area of investigation

This species occurs in sand and gravel near the high water line in places greatly exposed to the surf. I have found it in the bay north of Klubbans biological station in coarse sand.

Occurrence in plankton

Trochophores have been encountered in June and July. Older stages have been found even till in January.

The larva ready to metamorphose (fig. 3)

As good descriptions of the earlier stages in this species already exist, they will be omitted here. A description of the large pelagic larva can, however, be appropriate, as mistakes concerning its identity has been made even in a couple of modern works.

A larva with 19 segments and a length of 1.90 mm and a width of 0.30 mm has been chosen as typical of this stage.

The prostomium is richly set with tactile cilia, of which one pair is longer and stronger than the others. Viewed from above the four bright red eyes are located in the form of a trapezium. The prototroch, nuchal organs, and parapodia are generically typical. Branchial anlages are lacking. Nototrochs are found from the third segment onwards and are at this stage composed of only one pair of ciliated cells per segment. (In older individuals their number is increased to six.) The telotroch is continuous dorsally. The tip of the prostomium is brick-coloured. Moreover there is a diffuse green pigmentation in the epidermis, which becomes more vivid towards the pygidium.

The vestibule and pharynx have a clear orange colour. The oesophagus, which merges into the stomach in segment 3, has a green pigment. The stomach, which has strongly developed segmental diverticula, is pigmented chocolate brown. A short rectum is found. The pygidium is pigmented green. The larval setae are relatively short, lustreless, finely serrated, and

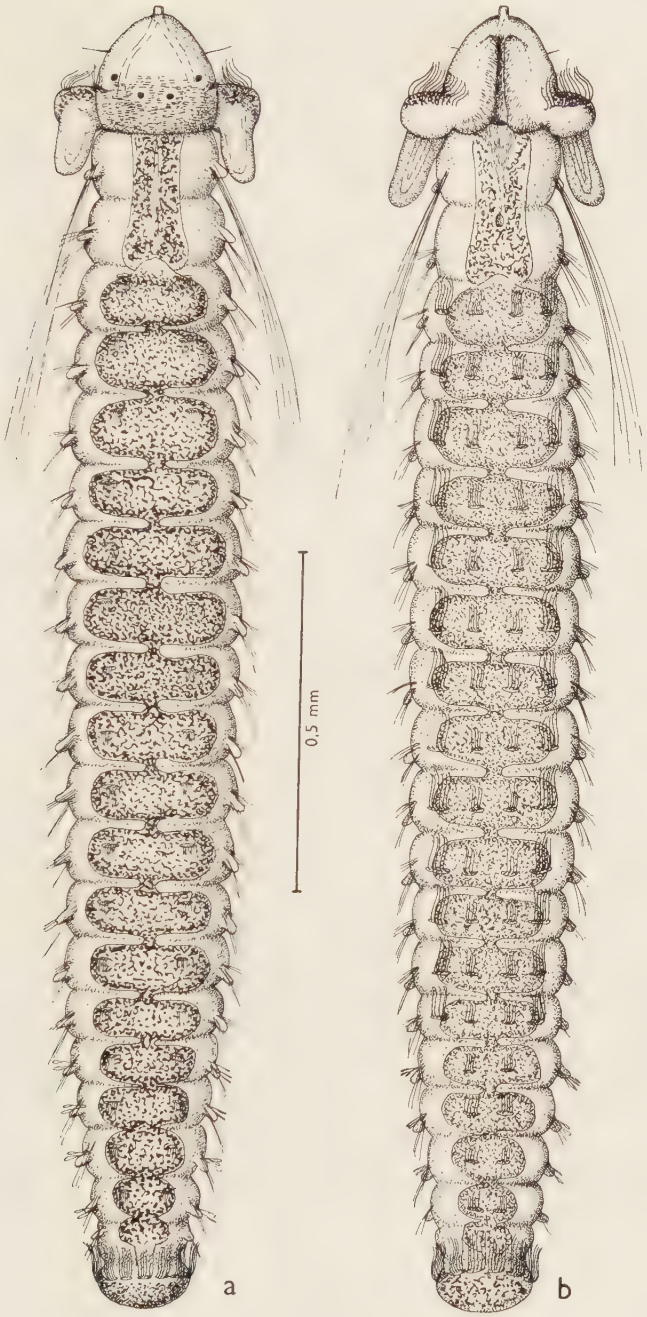


Fig. 3. *Nerine cirratulus* (Delle-Chiaje). Pelagic larva ready to metamorphose. a) Dorsal view. b) Ventral view.

are lost relatively easily. There are dorsal and ventral permanent hairy bristles in all segments. Ventral hooded crochets are found from segment 10 onwards and dorsal hooded crochets in the last segment. Both of these are diserrated. A neurotroch and a "ciliated pit" are observed. Gastrotrochs are found from the third segment onwards. In the anterior segments each is composed of four ciliated cells, in the posterior of two.

Biology

The larva metamorphoses in clean mineral sand and burrows without forming any resistant tube. It is apparently ready to metamorphose when it has grown to about 20 segments. On several occasions, however, larvae with 28–30 segments have been obtained in plankton.

Literature

Busch (1851, pp. 65–67, Pl. VIII figs. 1–4) described a larva which possibly can be referred to this species. Claparède et Mecznikow (1869 pp. 173–177, Pl. XII, figs. 1–4) were the first to describe the egg with the typical egg-membrane and membrane vesicles. Furthermore, they gave a description of a 30-segment larva which was illustrated by an excellent reproduction. The serrations of the larval setae have, however, probably been exaggerated, which made Häcker (1896) doubtful of the identification of a larva found by him in Naples. This should, however, most likely be classified here. Mesnil (1896) followed the entire development from the egg to the large pelagic larva. His pictures are, nevertheless, rather lacking in details. The larvae determined by Hofker (1920, 1930) as *Nerine cirratulus* probably belong to *Spio martinensis* Type I (see p. 84). Thorson (1946) identified a *Nerine cirratulus* larva as *Nerine foliosa* (p. 16). Everything goes to prove that the "*unknown spionid larva*" described by Smidt (1951, p. 99, fig. 36 B) should be referred to this species. The larva found by Ehlers (1913) near the Cape Verde Islands, which he suggested might be classified here, probably belongs, however, to a closely related species. His larva had a length of 4 mm and had 55 segments. Furthermore, it had ventrally in the anterior segments strongly developed needle-like bristles, which have not been seen in the *Nerine cirratulus* larva treated here. In conformity with the latter Ehler's larva had, however, ventral hooded crochets from segment 16 onwards.

Nerine sp. I

Occurrence in plankton, size, and general characteristics

This larva has been obtained in plankton on two occasions only, viz., September 16, 1952 and August 22, 1953. Only four specimens have been

obtained in all. A specimen with 10 segments had a length of 0.96 mm and a width of 0.36 mm. The larva does not appear to increase in growth appreciably before it is ready to metamorphose. The larva is characterized by green pigment and by a very large pygidium.

The 10-segment larva (fig. 4)

The prostomium and peristomium are of the usual *Nerine* type (p. 8). Anlages to palpi are lacking. The eyes are red and located in an approximately straight line when seen from above. The prototroch is well developed and nuchal organs are found. The peristomium forms a callosity over the "head". The parapodia are slightly differentiated with the exception of a very long tapered and somewhat curved dorsal cirrus in all segments. Nototrochs are completely lacking. The pygidium is very broad and of the same horseshoe-shaped type as in *Nerine* sp. II (p. 21). The larva is very slightly pigmented in the epitelium but very markedly in the alimentary canal. The oesophagus has a greenish yellow colour and extends through the second segment where it merges into the yellowish brown-pigmented stomach, which has slight segmental constrictions. The pygidium is pigmented yellowish green. The larval setae are robustly developed, somewhat curved and in section quadrangular. Three of the edges of the bristle are finely serrated, while the fourth is smooth (fig. 4d). Bristles of adult type are completely lacking. The neurotroch is surrounded in segment 1 by a pair of ciliated cells. The gastrotrochs are each composed of six ciliated cells.

The young benthonic stage (fig. 4e–f)

A large larva metamorphosed in clean mineral sand. It was examined after 50 days and at that time had 53 segments.

The prostomium was sharply tapered and the lateral parts of the peristomium were no longer clearly demarcated from the prostomium. The eyes were unchanged. A pair of relatively short palpi had been formed. All segments had developed both dorsal and ventral cirri, and branchiae were found in segments 2–27. They were well developed and slightly coalesced with the dorsal cirri. The pygidium was of the usual *Nerine* type. The oesophagus, which extended through segment 16 was unpigmented, and the stomach was pigmented brown. A convoluted rectum had been differentiated. The epidermis was pigmented a pale yellowish green throughout. Dorsal and ventral adult bristles occurred in all segments. Triserrated ventral hooded crochets were found from segment 18 onwards. In a side-view they appeared to be diserrated, as the two distal serrations covered each other. Dorsal hooded crochets were found in the most posterior segments. The serration was of the same type as in the ventral.

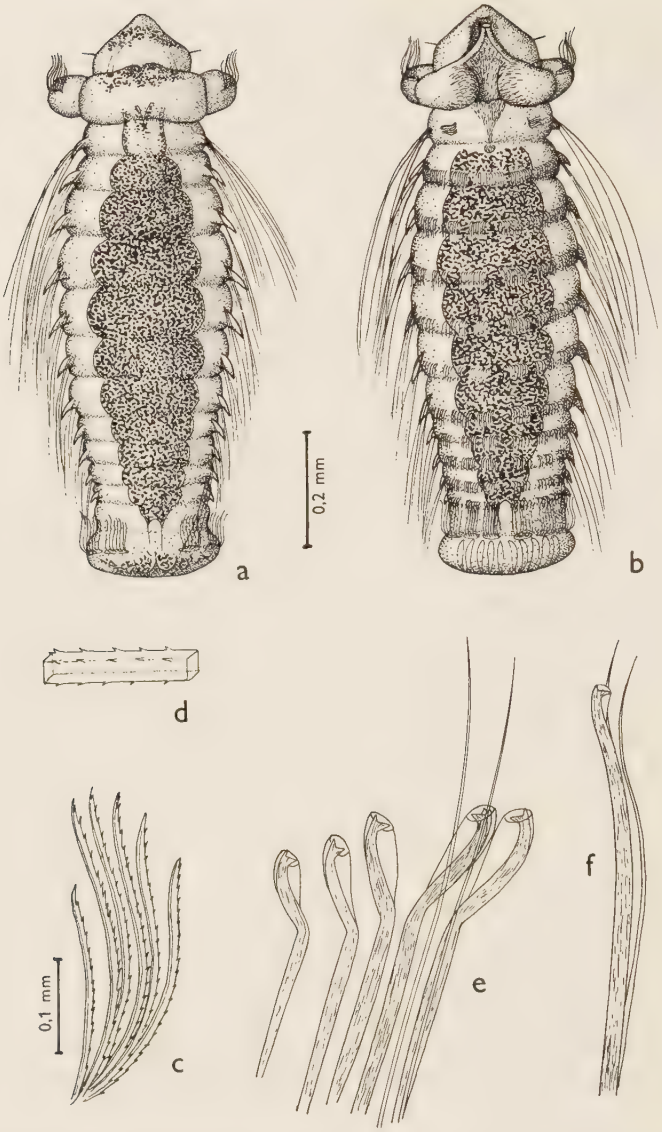


Fig. 4. *Nerine sp. I.* a) and b) Dorsal and ventral view of a pelagic larva. c) Larval setae. d) Detail of a larval seta showing the distribution of the serrations. e) Ventral hooded crochets from a recently metamorphosed worm. f) Dorsal hooded crochet from the same.

Identity of species

Nothing is known about the closer identity of the species.

Nerine sp. II

Occurrence in plankton, size, and general characteristics

This larva is very seldom encountered in plankton and I have observed

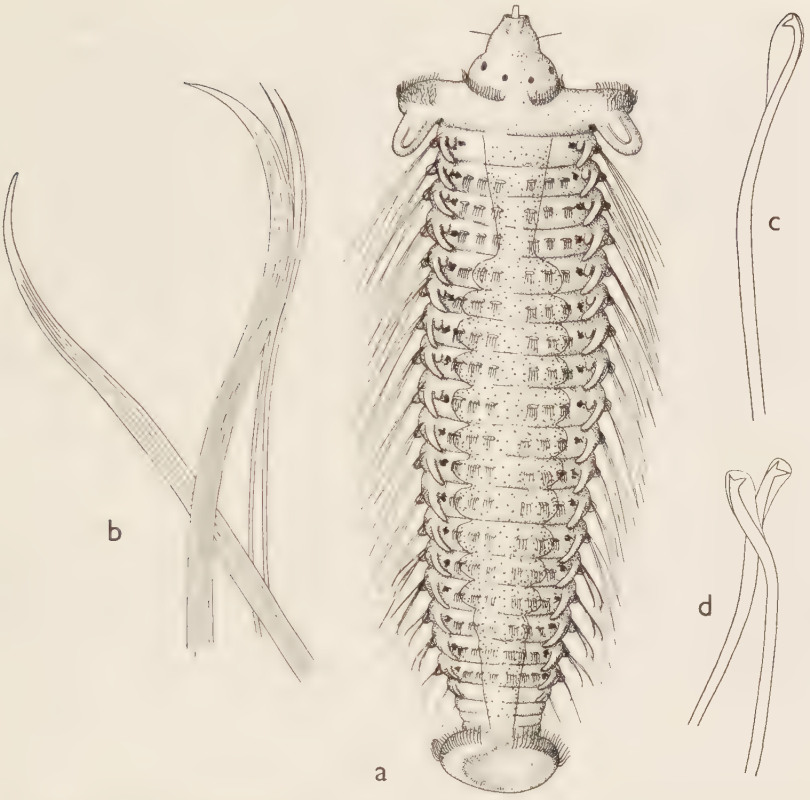


Fig. 5. *Nerine sp. II,* a) Pelagic larva (dorsal view). b) Dorsal curved setae from segm. 14 of the larva. c) Dorsal hooded crochet from the larva. d) Ventral hooded crochets from the larva.

it on three occasions only, viz., July 20 and 21, 1948, and June 24, 1953. The last-mentioned specimen had about 20 segments, a length of 2.10 mm and a width of 0.50 mm. This big larva is primarily characterized by two rows of red pigment spots along the dorsal side, and by large, curved, and smoth bristles of adult type in the most posterior segments.

The 20-segment larva (fig. 5)

The prostomium and eyes are of the usual *Nerine* type. The lateral parts of the peristomium (see p. 156) are, however, very much more robust than I have seen in any other larva. Laterally on the peristomium there is a pair of insignificant palpi. A pair of strongly ciliated nuchal organs is placed at the transition between the prostomium and peristomium. The prototroch, which is attached far out on the lateral parts of the peristomium, is weak. The dorsal cirri are very long, relatively thin, and tapered. Branchial anlages occur from segment 1 onwards. Nototrochs are visible starting from the second segment. Each nototroch consists of six ciliated cells. The pygi-

dium is robustly developed and has a dorsal notch. The telotroch is robust. The dorsal pigmentation is characteristic. In each segment except the last three or four there is laterally on either side a small intensive red pigment spot surrounded by diffuse melanin. The lateral parts of the peristomium and the pygidium are pigmented reddish brown. Otherwise the larva is transparent yellowish brown. The oesophagus extends through segment 4. The stomach has distinct lateral diverticula. The rectum is not clearly differentiated. The larval setae are short, somewhat curved, and relatively strong. In the posterior segments are observed dorsal, very well-developed and extremely curved bristles (fig. 5b), which in contrast to the larval setae are completely smooth. These bristles appear to be of a permanent type. From segments 15-16 rise ventral hooded crochets (fig. 5d) and in the most posterior segments also dorsal hooded crochets (fig. 5c).

Identity of species

I do not know anything about the closer identity of this species. To my knowledge no *Nerine* species has been encountered in our region which is provided with the robustly developed and curved bristles mentioned in the foregoing.

Laonice Malmgren

The egg and sperm

The egg has a thick egg-membrane and membrane vesicles, and is lentiform. The sperm is of the short-headed type.

The pelagic larva

The prostomium is stumpy and somewhat notched at the tip. The lateral parts of the peristomium are well demarcated from the prostomium. The palpi remain relatively undeveloped and are attached far out on the lateral parts of the peristomium. The prototroch is well developed. There are two pairs of red eyes. Dorsal organs are not developed. In section the body is four-cornerd and relatively thick in relation to its length. Branchial anlages and nototrochs are lacking in all pelagic stages. The telotroch is well developed and dorsally discontinuous. There is no pigmentation exept in the eyes. The larval setae are of a very special type ("*Chaetosphaera*"-bristles, Fig. 6d). A ciliated pit is formed in segment 2. In older larvae gastrotrochs occur in all segments from the third onwards.

Key to species

1. One species, characterized in the foregoing. *Laonice cirrata.*

Laonice cirrata (Sars)

Occurrence in the area of investigation

Laonice cirrata (Sars) has been divided by Söderström (1920) into four species, viz.: *L. bahusiensis*, *L. appelöfi*, *L. sarsi*, and *L. cirrata* s.str. Later investigators have, however, been unable to find any justification for such a division (Fauvel 1927). Since I have found only one larval type which can be referred to this species, I feel obliged to describe it under *L. cirrata* (Sars). Söderström reports that two of his *Laonice* species are found in the area of investigation, viz. *L. bahusiensis* and *L. sarsi*. I myself have found *Laonice* at a depth of about 50 meters in the outer part of the fjord and also on shell gravel at a depth of 15 m near the island Bonden.

Occurrence in plankton

Strangely enough this larva occurs in plankton during two widely separated periods. The first covers January and the beginning of February, the second August and September with occasional specimens in October and November. As mentioned in the foregoing Söderström (op. cit.) found two of his *Laonice* species in the Gullmar fjord, and one might surmise that the spring larva represents one species and the autumn larva the other. No morphologic differences could, however, be ascertained between these larvae.

Size of the pelagic larva

Segments	Length mm	Width mm
4	0.30	0.11
8	0.43	0.14
14	0.80	0.20
18	0.90	0.22

The pelagic larva (fig. 6)

The prostomium is richly set with tactile cilia. In dorsal view the four red eyes are located on an approximately straight line. The lateral ones are also relatively ventrally situated. The lateral parts of the peristomium form dorsally a pair of thin integumental flaps which are directed towards the median line. Their inner tips are tapered and free. There is a small, stumpy, occipital tentacle. The parapodia are weakly differentiated and do not develop short stumpy anlages to cirri until relatively late. Pigmentation is lacking except in the eyes. The alimentary canal has a pharynx, which in a 14 segment larva extends through the second segment, followed

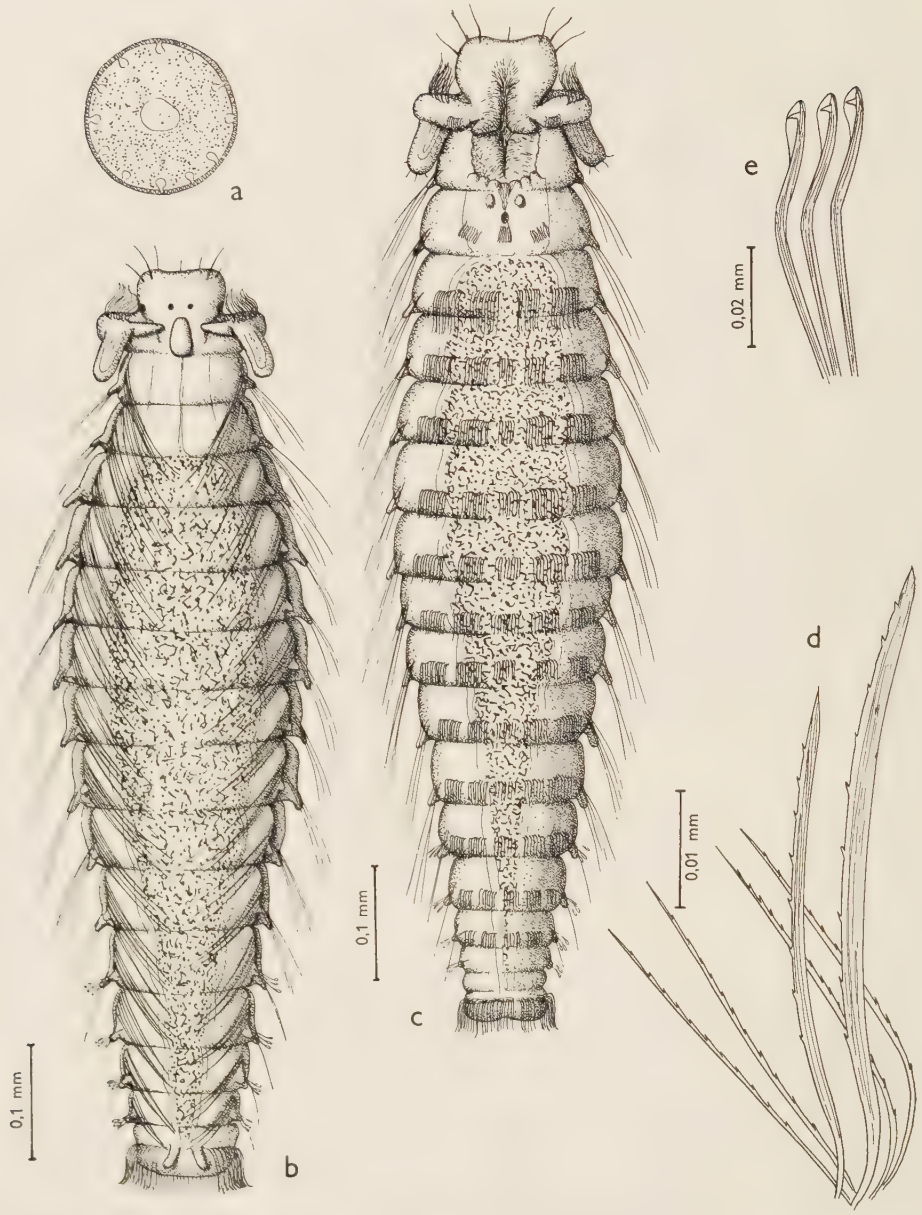


Fig. 6. *Laonice cirrata* (Sars). a) Egg. b) Pelagic larva (dorsal view). c) Pelagic larva (ventral view). d) Larval setae. e) Ventral hooded crochets from a pelagic larva.

by the voluminous stomach which has only very small segmental diverticula. It has always green or yellowish green contents. The rectum is always very short and straight. The vestibule is relatively complex. The lateral portions of the peristomium are attached to the lateral lips by narrowed parts.

These narrowed parts contains each a ciliated cell. The lateral lips are relatively small. The ventral lip is greately retracted in its median portion, almost to the boundary between segments 1 and 2. In this manner the mouth acquires cross-shape. The inside of the vestibule is richly ciliated. The entire posterior part of the vestibule bears a certain resemblance to that in the *Disoma* larva (fig. 51 c). The neurotroch is narrow and surrounded in its anterior part by a pair of rounded ciliated swellings (see p. 162). On both sides of a "ciliated pit" there is a ciliated cell. In the young larva gastrotrochs are found only in segments 3 and 5. Such an arrangement is otherwise encountered only in g. *Scolelepis* and subfam. *Spioninae* (see p. 160). The larval setae are of a very special type (fig. 6d). They are found in the notopodiae as well as in the neuropodiae. All bristles are flattened and curved, and unilaterally serrated. Two of the dorsal ones in each parapodium are broader and sabre-shaped, the others are narrower. Ventrally there are bristles of the narrower type only. Of adult bristles there are dorsal as well as ventral hairy bristles in all segments and from segment 14 onwards also ventral hooded crochets (fig. 6e). The last mentioned are diserrated and the distal serration forms a large angle with the proximal. One or two of these characteristic bristles are found in each neuropodium.

Identity of species

In spite of a great number of breeding experiments it has not been possible to get this larva to metamorphose.

Several facts speak, however, in favour for *Laonice:*

1. An occipital tentacle is formed.
2. Pygidial cirri are formed in the oldest larvae.
3. The characteristic ventral hooded crochets agree in all respects with those found in the adult *Laonice.*
4. No other larva, which can reasonably be classified under *Laonice*, has been encountered during the course of investigation. This genus should have a pelagic development. The egg type supports this view (fig. 6a, see p. 179).

Literature

Häcker (1898, pp. 19–20, Pl. III, figs. 21 and 22) described a larva which he named "*Chaetosphaera*". He characterized its larval setae as follows: "...während in den dorsalen Borstenköchern Strahlfächer von 5–6 grösseren und kleineren, sichelförmigen an den konvexen Seiten fein gezähnelten Borsten steckt. Die Spitzen dieser Borsten sind mehr oder weniger nach der konvexen Seite zurückgebogen, sodass wenigstens die grösseren derberen Borsten, von den je 2 3 in jedem Büschel stehen, annähernd die Gestalt eines Bumerangs besitzen...". As we have seen, this description

agrees well with the larval setae of *Laonice cirrata*. Since his larvae, which are relatively short and thick, have two pairs of eyes, etc., it is very probable that the "*Chaetosphaere*" larva should be classified under this genus. The "*Chaetosphaera*" larvae from the Antarctic described by EHLERS (1913) are most likely closely related to HÄCKER's. Their larval setae diverge, however, somewhat and one of them is considerably larger. All these larvae have, nevertheless, broad and flat larval setae which appear notopodially as well as neuropodially. GRAVELY (1909 B, p. 45) also described a larva among whose setae he found "...single, broad, flat and somewhat curved setae, with rather finely serrated edges...". He classified this larva as "*Chaetosphaera*". FAUVEL (1916) has a rather complete description of a "*Chaetosphaera falconis* Häcker", to which he does, however, assign no place in the system. Finally HOFKER (1920) briefly described a "*Chaetosphaera*" which can be identical with the one treated here. He characterized the larval setae as "de kromme sabels der Turken". He suggested that the larva should belong to *Polydora hoplura*.

Aonides Claparède

The egg and sperm

The egg is spherical and provided with a thick egg-membrane and one or two rows of "membrane vesicles" in a circle at right angles to the future longitudinal axis of the larva. The sperm is of the short-headed type and has a relatively tapered acrosome.

Type of development

The development is entirely pelagic and lecithotrophic.

The pelagic larva

The pelagic larva is distinguished in all stages by its abundant yolk, which gives it a yellowish opaque appearance. Two pairs of red eyes are formed. Branchial anlages are not developed. Pigmentation is lacking except in the eye spots. The larval setae are long and straight. Gastrotrochs are found in all segments from the second onwards.

Key to species

Larval setae strongly developed and coarsely serrated. *Aonides paucibranchiata* (p. 30).
Larval setae thin and slightly serrated. *Aonides oxycephala* (p. 26).

Aonides oxycephala (Sars)

Occurrence in the area of investigation

This species is found near the island Bonden in shell gravel (G. GUSTAFSON, verbal communication).

Occurrence in plankton

A small number of larvae, about 60 in all, have been collected during August and September 1952 and 1953.

Size of the pelagic larva

Stage	Length mm	Width mm
Young trochophore (including membrane)	0.40	0.30
Older trochophore (including membrane)	0.48	0.24
8 segments	0.80	0.20

The young trochophore (fig. 7a)

At this stage the larva does not completely fill the egg-membrane. The latter has the form of an hour-glass with a constriction where the prototroch will subsequently be formed. The membrane is thick with transversely striated structure. Around both the upper and lower halves there is a row of membrane vesicles. The larval prostomium is tapered. At the constriction of the egg-membrane there is a pair of lateral elevations, which represent anlages to the lateral parts of the peristomium. The extremity is stumpy. There is no evidence of segmentation. Neither the prototroch nor the telotroch are discernible at this stage.

The older trochophore (fig. 7b)

In this stage the egg-membrane is filled to a considerably higher degree than in the foregoing. The prostomium has been notably broadened and has acquired a distinct apical tuft. The lateral parts of the peristomium have grown and are now well demarcated from the prostomium. A pair of red eyes has been formed. A prototroch which is discontinuous dorsally, and a telotroch have appeared. The egg-membrane has stretched but is still not completely filled out by the body. There are still marks after the double row of vesicles. No segmentation can as yet be detected. Bristles are completely lacking. The larva is still opaque due to the abundant yolk.

The 8-segment larva (figs. 7c–d)

The development from the first stage described to this one is relatively fast, probably occupying only a few days, not more than a week. During this period the larva subsists entirely upon the yolk of the egg.

Not even in this stage has the egg-membrane been completely filled out by the larval body but is free from it at the prostomium and the pygidium.

The prostomium is rounded and bears apically a pair of small tactile cilia. An additional pair of red eyes has appeared, viz. the lateral ones which are placed also relatively ventrally. The peristomium is weak and the lateral parts are now not particularly demarcated from the prostomium. They support a well-developed prototroch which is provided with interspersed tactile cilia. A pair of nuchal organs are visible. The parapodia and the pygidium are very slightly differentiated and lack cirri. The telotroch is well developed. It could not be decided whether nototrochs occur or not. Pigmentation is lacking except in the eyes. In the vestibule the lateral and ventral lips have been formed. No certainty could be reached as to the occurrence of a "ciliated pit" or a neurotroch. Gastrotrochs are found in all segments from the second onwards. An undifferentiated alimentary canal is noticeable, but ingestion of food has not yet begun. The larva is still relatively opaque due to its abundant yolk. Larval setae have been formed and are found in all segments. In the first segment they are very long and extend beyond the pygidium when posteriorly directed. In the succeeding segments they are considerably shorter. Adult bristles are found, and among them diserrated hooded crochets (fig. 7f).

In a late 7-segment stage (fig. 7d) the egg-membrane had been completely filled out and formed the larval cuticle. This larva had begun to loose its trochs and larval setae. The palpi had increased in length, and the parapodial cirri had started to develop. The gut had begun to be differentiated but no food had been ingested so far.

The young benthonic stage (fig. 7e)

The description is based on a number of individuals examined one month after metamorphosis, which took place in sandy mud. The largest specimen had 22 segments and a length of 2.5 mm.

The prostomium has been considerably extended and has acquired at the tip a very slight notch. The eyes are still four in number. The palpi have grown vigorously. They are set with short stiff hairs. Posteriorly the prostomium has been drawn out into a very narrow "crest", which extends to the boundary between segments 1 and 2. On both sides of this crest there are a pair of large nuchal organs (in the smaller oval-shaped, in the larger V-formed with the apex posteriorly orientated). The parapodia have grown and are well differentiated. Both dorsal and ventral cirri are found in all segments. The ventral cirri are oval leaf-shaped and decrease posteriorly in size. The dorsal cirri in segment 1 are very small. In segment 2, however, they are large leaf-shaped and triangular, and have a pronounced tip. In the smaller individuals the outer edges of the dorsal cirri are crenated. This crenation disappears in older ones. In these there are also branchiae in segment 2. Nototrochs are found in all segments from the second on-

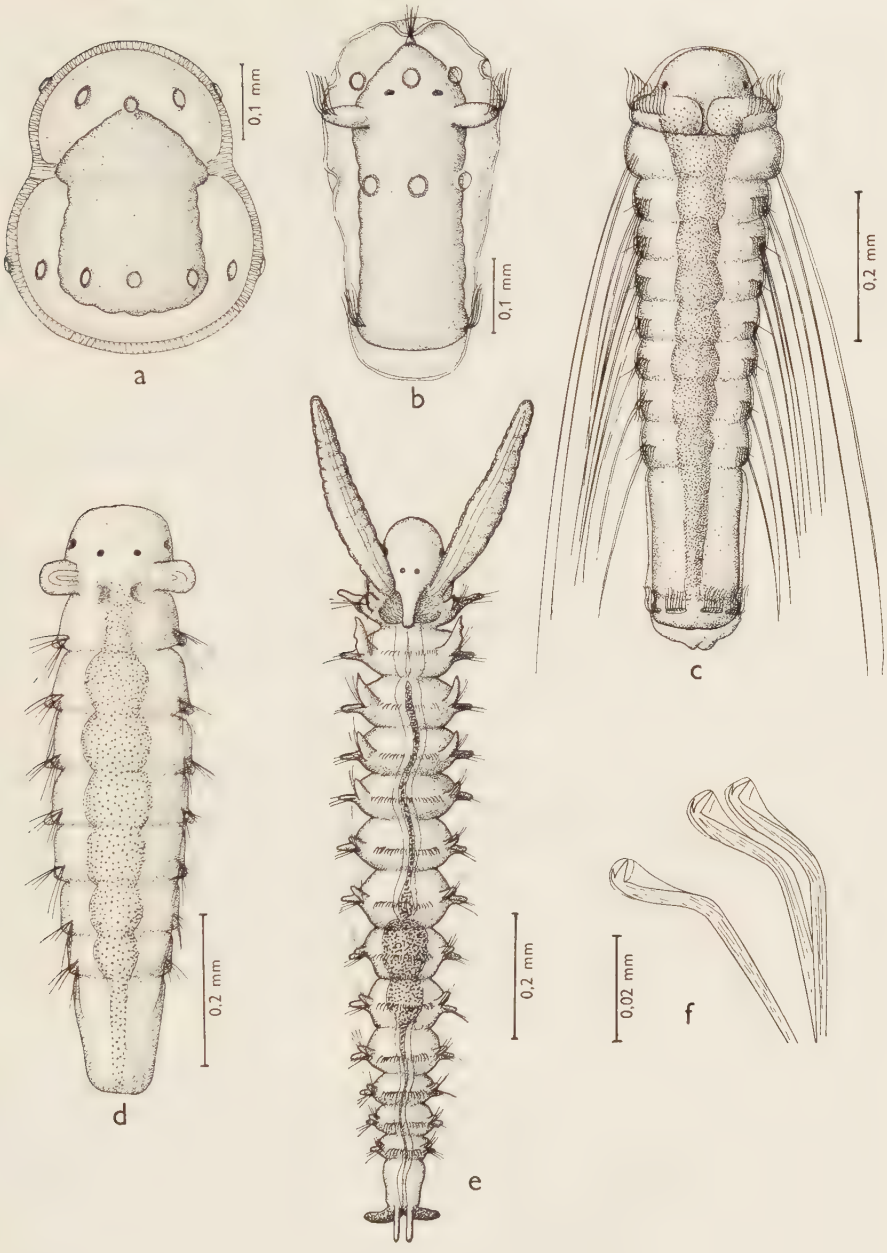


Fig. 7. *Aonides oxycephala* (Sars). a) Young trochophore. b) Older trochophore. c) Pelagic larva ready to metamorphose (ventral view). d) Metamorphosing larva (dorsal view). e) Bottom stage one month after metamorphosis. f) Ventral hooded crochets from the specimen in e.

wards. The pygidium has four cirri. The ventral ones are short, thick, brown-pigmented and laterally orientated. The dorsal ones are long, narrow, unpigmented and posteriorly directed. Pigmentation is totally lacking except in the eyes and the pygidium. The "pharynx" is followed in segment 2 by a long and thick-walled anterior gut section extending through segment 7, where a very short stomach begins. This does not extend beyond segment 9. The rectum is somewhat convoluted. Dorsal and ventral hairy bristles are found in all segments. From segment 9 onwards there are three ventral hooded crochets in each neuropodium. They are noticeably curved and diserrated (fig. 7f).

Identity of species

By reason of the size and the form of the dorsal cirri, and of the appearance of the pygidium and the crochets I do not hesitate to classify this larva as that of *Aonides oxycephala*.

Aonides paucibranchiata Southern

Occurrence in the area of investigation

The species is found near the island Bonden in shell gravel (Söderström 1920; G. Gustafson, verbal communication).

Size, general characteristics, and occurrence in plankton of the pelagic larva

This larva has only been obtained on two different occasions, viz. October 15, 1951 and October 13, 1952. The first-mentioned specimen had 9 setigers, a length of 0.76 mm and a width of 0.18 mm; the second specimen 7 setigers, a length of 0.62 mm and a width of 0.16 mm. Like the preceeding larva this one is characterized by its abundant yolk. It differs, however, by its more strongly developed larval setae which are coarsely dentate.

The pelagic larva (fig. 8)

The peristomium is moderately set off from the prostomium, and on its lateral parts a pair of palpi are attached. Terminally the prostomium has a slight notch. A pair of transversely placed, finely ciliated grooves represents nuchal organs. The prototroch is well developed and attached far out on the lateral parts of the peristomium. The parapodia are well demarcated from the body and bear small anlages to cirri, both dorsally and ventrally. In segments 2–6 the ventral cirri are stronger than in the other segments. Nototrochs occur from the second segment onwards and are probably composed of only one pair of laterally set ciliated cells in each segment. In the pygidium two pairs of cirri are developed. The ventral ones are very short and broad. The dorsal ones, on the other hand, are

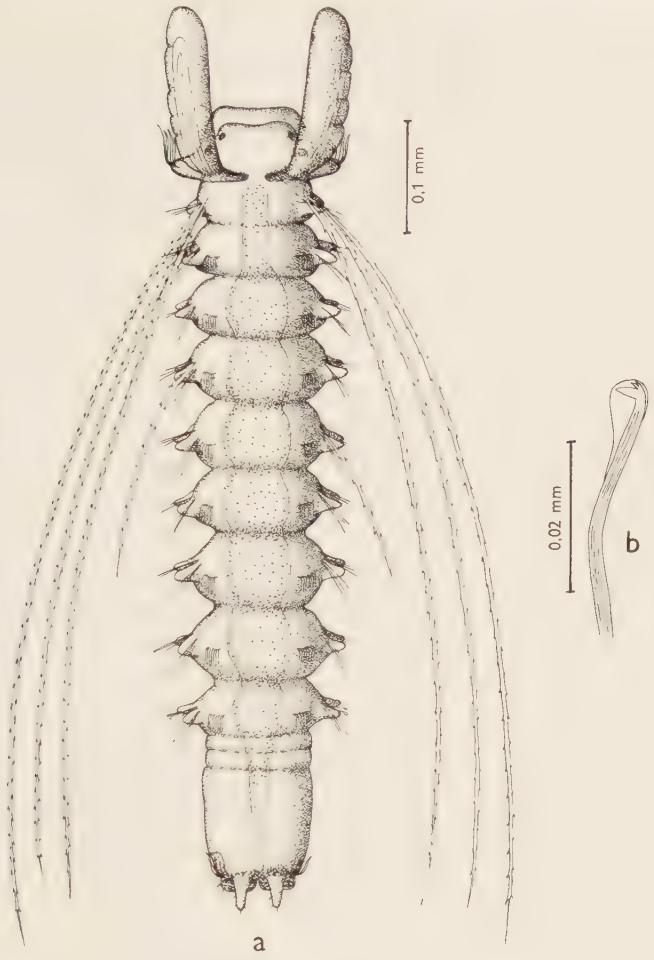


Fig. 8. *Aonides paucibranchiata* Southern. a) Pelagic larva (dorsal view), b) Ventral hooded crochet from this larva.

long, narrow, and caudad directed. A rather weak telotroch is discernible. The larva is opaque yellowish white due to the abundant yolk. Pigment is lacking with the exception of the eyes and a slightly diffuse brown pigment on the pygidium. The gut is very slightly differentiated, and the larva does not ingest any food. The larval setae are very long (as long as the entire larva), strongly developed and coarsely serrated. Of adult bristles there are both dorsal and ventral hairy bristles in all segments. In the most posterior segment of the larger specimen there were also triserrated hooded crochets (fig. 8b). Gastrotrochs probably occur in all segments from the second, onwards.

Identity of species

Great similarities exist between this larva and the one I have classified as *A. oxycephala*. It is rich in yolk like the latter, and has a pygidium of the same type as encountered in the benthonic stage of this species. Most likely the larva should be referred to this genus. Both *A. oxycephala* and *A. paucibranchiata* are known from the area of investigation. Already for this reason one is inclined to refer the larva to the latter species. As the larva has, moreover, triserrated hooded crochets of a type which is characteristic for this species, I consider it very probable that the larva belongs to *A. paucibranchiata*.

Literature on Aonides development

Claparède (1864, pp. 47–48, pl. 3, fig. 3) described the egg and sperm of *Aonides auricularis*. He found the egg to be spherical and surrounded by a thick egg-membrane with small elevations on the surface. It also had a row of vesicles surrounding the egg equatorially. The sperm had a relatively short head and was provided with a rather tapered acrosome. Fauvel (1916) has described three larvae which he provisionally referred to this genus. They have several properties in common with those treated here. They are exceedingly rich in yolk, and are provided with larval setae of the type encountered in *A. paucibranchiata*. Furthermore, they have ventral hooded crochets of the same type as this species. Rioja (1938) described a larva from Mexico with larval setae which resemble those of *A. paucibranchiata* in a very high degree by being coarse and set with large serrations. Unfortunately he has figured only the anterior part of the larva. He considered that this larva should be referred to *Aonides*, although his reasons for this decision were not given.

Spiophanes Grube

The egg and sperm

The egg has a thick membrane and membrane vesicles, and is lentiform. The sperm is of the short-headed type.

Type of development

The development is presumably entirely pelagic and predominantly planctotrophic.

The pelagic larva

The lateral parts of the peristomium are well demarcated from the prostomium. The palpi remain relatively short and are attached far out on the lateral parts of the peristomium. The prototroch is well developed.

There are two pairs of red eyes. Branchial anlages are lacking in all pelagic stages but nototrochs are found. The pygidium is rounded and is equipped with numerous cirri in older larvae. The telotroch is well developed and dorsally discontinuous. The larval setae are thin and lustreless. In old larvae the generically typical curved bristles in segment 1 are developed. Gastrotrochs occur in all segments from the third onwards. The "ciliated pit" is located in segment 2.

Key to species

1. Yellow pigment on the prostomium and pygidium. In old larvae lateral processes on the prostomium are developed. Black pigment in the pharynx and the proctodaeum. *Spiophanes bombyx* (p. 33).
   Yellow pigment completely absent. No lateral processes on the prostomium in old larvae. Pharynx and proctodaeum reddish brown pigmented. *Spiophanes kröyeri* (p. 36).

Spiophanes bombyx (Claparède)

Occurrence in the area of investigation

The species occurs on sandy bottom mixed with mud. Söderström (1920) found it at a depth of 10 30 m in the Vasholme Fjord south of Gåsö. I have found it at a depth of 1 m in the bay of Kristineberg.

Occurrence in plankton

The larva appears sometimes in very great numbers during the period April–December. In certain years, however, it is very rare (see p. 183).

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
10	1.05	0.22
12	1.10	0.24
14	1.40	0.24
19	1.90	0.30

The larva is easily recognizable by the intensive yellow colour on the prostomium and pygidium, and also black pigment in the pharynx and proctodaeum. It has a characteristic angular position when swimming.

The larva ready to metamorphose (fig. 9a and b)

As typical of this stage an individual with 15 setigers is described.

The prostomium is stumpy, and medially there is a slight notch. Laterally it bears two processes (lacking in younger individuals). There are two

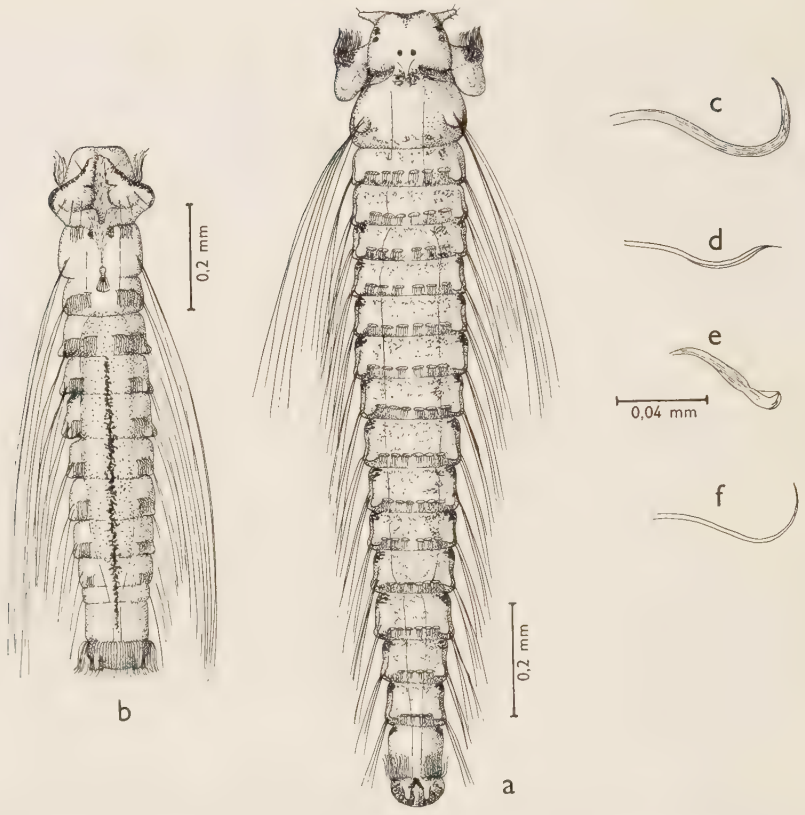


Fig. 9. *Spiophanes bombyx* (Claparède). a) Pelagic larva ready to metamorphose (dorsal view). b) Somewhat younger larva (ventral view). c) Ventral curved bristle from segment 1 of a recently metamorphosed worm. d) Ventral "winged" bristle from segment 2 of the same. e) Ventral hooded crochet from the same. f) Curved bristle from middle segment of the same.

pairs of red eyes. The lateral ones are situated somewhat anterior and ventral to the median ones. The nuchal organs have the form of a pair of sickle-shaped, ciliated grooves. In the parapodia there are anlages to both dorsal and ventral cirri. In the middle part of the body the generically characteristic parapodial glands are found. Nototrochs occur from the second segment onwards. They are each composed of six cells. Dorsally and ventrally in the pygidium there are indications of cirri. The dorsal side exhibits a very diffuse melanin pigmentation and laterally a brick-red pigmentation. Pigment of this type is also found on the lateral parts of the peristomium and on the pygidium. An intensive yellow pigmentation (reflected light) is formed on the prostomium and pygidium. The pharynx and oesophagus extend through segment 3. The inside of the pharynx has a pair of black or blackish brown pigment spots. The vestibule has a cross-shaped opening (fig. 9b). The lateral lips have among finer ciliae also longer

tactile ones. On both sides of the neurotroch in segment 1 there is a pair of large ciliated cells. The gastrotrochs in segments 2–3 are robustly developed and consist of four large ciliated cells. The following gastrotrochs are somewhat weaker and are composed each of only one pair of small ciliated cells. The larval setae are not especially long and are lustreless.

The metamorphosis apparently can take place when the larva has attained a size of 16–18 segments.

The young benthonic stage (figs. 9c–f)

The description of the recently metamorphosed worm is based primarly on a specimen which had 18 segments and a length of 1.30 mm.

The lateral processes of the prostomium are considerably more pronounced than in the larva. The palpi are still rather undeveloped but have a rich ciliation. The nuchal organs have the form of a pair of oval ciliated fields, and extend to about the boundary between segments 1 and 2. Medially they are separated by a very narrow nuchal crest only, which is posteriorly slightly furcate. Nototrochs are found from segment 2 onwards. The parapodia have undergone a marked differentiation. Up to and including segment 4 the ventral cirri appear narrow in dorsal view. Thereafter follows a section of the body which extends through segment 12 and in which parapodial glands occur. Here the cirri observed from above are broad and robustly developed. Caudal to this part the ventral cirri again become smaller. Branchiae are lacking. The dorsal cirri in segment 1 are small, in the following segments relatively long and tapered. Posteriorly they become gradually shorter. The pygidium has three pairs of cirri (in one specimen, which was as large as the one described here, there were only two pairs). The entire larval pigmentation remains unchanged. The oesophagus extends through segment 5. The stomach possesses an abundance of oil drops. The proctodaeum is short and straight. Both ventral and dorsal hairy bristles are found in all segments. In segment 1 the characteristic curved bristles of this genus are observed (fig. 9c), and from segment 13 onwards ventral hooded crochets (fig. 9c).

Identity of species

By reason of the absence of branchiae in the benthonic stage, the occurrence of the typical parapodial glands in the middle section the genus must be established as *Spiophanes*. The occurrence of lateral processes on the prostomium is sufficient for determining the species as *S. bombyx*.

Biology

It is possible to get the larva to metamorphose in pure sand as well as in mud. The benthonic stage forms thin hyaline tubes which are not very resistent.

Literature

The egg has been described by Claparède (1870). In 1896 Mesnil gave an excellent description of the larva accompanied by a number of drawings. Of the more recent investigations McIntosh's (1915) and Thorson's (1946) may be mentioned. A faulty classification has been made by Smidt (1951, pp. 58–59, fig. 24 A–C). Here he designates as "*Pygospio elegans Type III*" a larva which is undoubtedly a *Spiophanes bombyx* larva. This is supported by the yellow pigment of the prostomium, the partly black-pigmented pharynx, formation of lateral processes on the prostomium, etc. (see also *Pygospio elegans*, p. 99).

Spiophanes kröyeri Grube

Occurrence in the area of investigation

The species occurs plentifully on mud bottom (40–90 m) in the Gullmar Fjord.

Occurrence in plankton

The species spawns during the winter months, and has regularly been observed in plankton from the end of November until the end of February. Occasional specimens have been obtained in March and April, and also in September and October.

The egg and sperm

The egg is circular, has a diameter of about 160 μ and a thickness of about 20 μ. There are 30–40 membrane vesicles. It is reddish in colour The sperm is of the short-headed type.

The early development

Regarding the fertilization the reader is referred to p. 153. The cleavage takes place very slowly at +6° C (the prevailing temperature in the natural biotop during spawning). In a couple of experiments it was ascertained that the first cleavage groove is formed 16–18 hours after fertilization, and after an additional 24 hours 8-cell stages can be observed. I have not succeeded in carrying the development farther than about the 60-cell stage, although the experimental conditions have been varied in diverse manners. The development is certainly entirely pelagic.

Size and general characteristics of the pelagic larva

Stage	Length mm	Width mm
Trochophore	0.20	—
6 segments	0.70	0.16
11 ,, ...	0.80	0.18
18 ,, ...	1.50	0.30
22 ,, ...	2.10	0.40

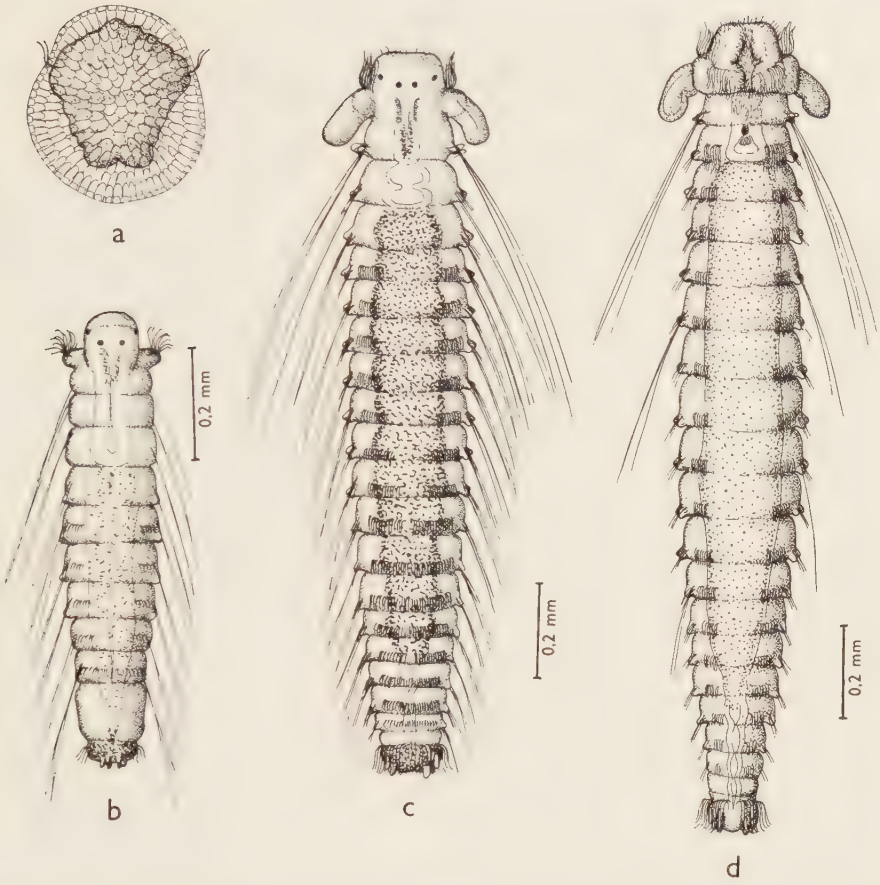


Fig. 10. *Spiophanes kröyeri* Grube. a) Trochophore presumably belonging to this species. b) Small pelagic larva (dorsal view). c) Big pelagic larva (dorsal view). d) Pelagic larva ready to metamorphose (ventral view). Larval setae partly shed.

The larva is characterized by being long and slender, and almost completely colourless. Reddish brown pigment occurs, however, on the pygidium and on the inside of the pharynx.

The trochophore (fig. 10a)

A trochophore probably belonging to this species was obtained in plankton on January 18, 1952.

The egg-membrane does not follow the body and has a more distinctly ridged structure than the egg. The membrane vesicles are still discernible on the lateral sides of the larva. A weak prototroch has been formed. The larva still has an abundance of yolk and the same reddish colour as the egg.

The larva ready to metamorphose (figs. 10c–d)

The description is based primarly on two individuals with 20 and 22 segments.

The prostomium is stumpy and lacks lateral processes. The red eyes lie in a straight line when observed from above. There are well developed tactile cilia on the prostomium. Palpi are still lacking in the 10-segment stage, but are developed here. The peristomium is not quite so sharply demarcated from the prostomium as in the foregoing species. The parapodia bear small anlages to cirri. Nototrochs occur from segment 4 onwards. In this and the 6–7 succeeding segments the nototrochs are composed of lateral ciliated cells only, but in the following they form complete transversal bands. In segments 4 and 5 there are anlages to parapodial glands. They are composed of curved, sausage-shaped formations, which extend far into the body. The reddish brown-pigmented pygidium bears six pairs of short cirri (already discornible in the 6-segment stage). Dorsal pigmentation is lacking except on the pygidium. The pharynx extends through the first segment, and the inside exhibits a characteristic reddish-brown pigmentation. Following the pharynx there is a short muscular oesophagus which extends through segment 2. The stomach, which most often has green contents, extends through segment 15. The rectum has strongly developed walls, is somewhat convoluted and most often pigmented reddish-brown. Of the adult bristles the characteristic curved ones in segment 1 are noticeable. There are, furthermore, dorsal and ventral hairy bristles in all segments, and ventral hooded crochets in the posterior part of the body. The "ciliated pit" is surrounded by two very large ciliated cells. The gastrotrochs are composed in all segments of only one pair of relatively weak ciliated cells. Ventrally pigment is lacking except in the pygidium.

The young benthonic stage (fig. 11)

The description is based primarly upon one individual with 21 segments, a length of 1.5 mm and a width of 0.30 mm.

The prostomium has become broader and flatter than in the larva and, terminally, has acquired a slight notch. The eyes are unchanged. Posterior to the medial pair of eyes a small occipital tentacle has developed. The palpi have increased greatly in length and when posteriorly directed they reach beyond segment 5. The nuchal organs, through posterior extension, reach to about the middle of segment 2. Nototrochs are found from segment 9 onwards. In the preceeding segments they are represented only by lateral ciliated cells. The pygidium still retains its larval pigmentation and bears three pairs of well-developed cirri. Of these the dorsal are biggest. Both dorsal and ventral cirri have been formed in the parapodia. From segment

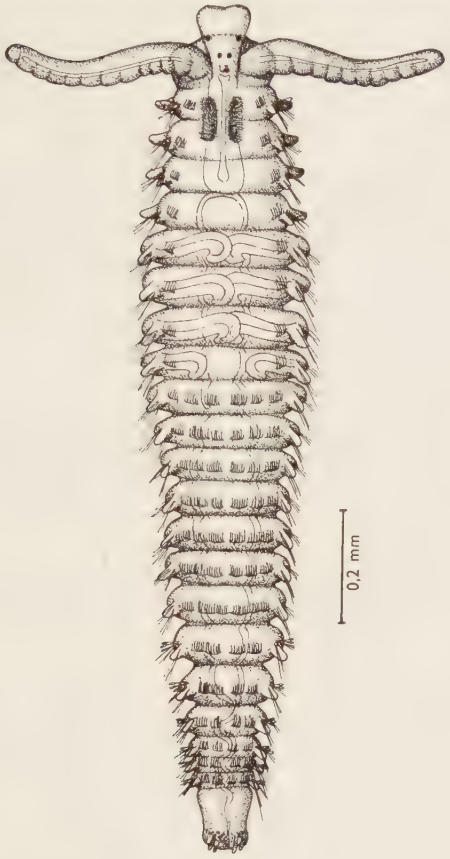


Fig. 11. *Spiophanes kröyeri* Grube. Young bottom stage (dorsal view).

5 onwards the neuropodia are broad and without ventral cirri. In segments 5–8 large parapodial glands have been formed. Of the adult bristles curved ones are found in segment 1, hairy bristles of two types (dorsal longer and ventral shorter) in all segments, and from segment 16 onwards ventral hooded crochets (two per neuropodium). The gut is not significantly altered.

Identity of species

By reason of the formation of curved bristles in segment 1, the absence of branchiae, the formation of an occipital tentacle, parapodial glands, and typical ventral hooded crochets the species must undoubtedly be established as *Spiophanes kröyeri*.

Biology

The larva swims partly with the help of its ciliae and partly (old larvae) by wriggling movements of the body. The latter way of swimming seems

to be uncommon among Spionid larvae. The larva like so many other mud-bottom species does not readily undergo metamorphosis in cultures. I have been successful only a few times although numerous attempts have been made.

Literature

THORSON (1946) described a larva which he presumed belonged to this species. This does not agree in any way with the one described here. It gives the impression, however, of being a *Sabellaria* larva (cf. v. DRASCHE 1885, CAULLERY 1914, and WILSON 1928).

Prionospio Malmgren

The egg and sperm

The egg is of the thick-membraned type. Membrane vesicles occur in small numbers or are totally lacking. The sperm has a short head and a tapered acrosome.

Type of development

The development is entirely pelagic and predominantly planctotrophic.

The pelagic larva

The body is long and slender. The prostomium is rounded. The lateral parts of the peristomium are not especially well demarcated from the prostomium. Two pairs of eyes are found. The prototroch is well developed. There is a very broad nuchal crest. The parapodia are differentiated at a relatively late date. Nototrochs are developed in the anterior segments of old larvae. The pygidium acquires up to three pairs of cirri. The larvae are relatively weakly pigmented. A "ciliated pit" is located in segment 1, 2, or 3. Gastrotrochs occur in all following segments. The larval setae are thin and lustreless.

Key to species

1. Red eyes. 2.
   Black eyes. 3.
2. Dorsally red pigment. Palpi are lacking or very insignificant even in large larvae. *Prionospio steenstrupi* (p. 46).
   Dorsally no pigmentation. The palpi become more developed. *Prionospio cirrifera* (p. 49).
3. Black eyes. Palpi are lacking or very insignificant. *Prionospio malmgreni* (p. 40).

Prionospio malmgreni Claparède

Occurrence in the area of investigation

The species occurs in very great numbers on soft bottoms at depth from about 40 to about 70 m in the Gullmar Fjord.

The egg and sperm

The egg is somewhat flattened and has a diameter of ca. 0.10 mm. The egg-membrane is relatively thick and has a finely sculptured surface. Membrane vesicles are completely lacking. The sperm has a total length of 0.10 mm. The head is very short and provided with a tapered acrosome.

Breeding period

Of 33 individuals examined from the Gullmar Fjord 11 proved to be females and 22 males. The sexual ratio should thus lie around 1 : 2. The pelagic larva is met with in plankton in July and August, when it sometimes occurs in very great numbers. The larva has been encountered earliest on June 30 (1948) and latest on September 8 (1951). Sexual products in the coelom of adult specimens, however, have been observed very much earlier. A male with active sperm was encountered as early as April 2 (1951). In the beginning of May 1951 a number of sexually mature individuals were collected and reared in cultures at room temperature. Spawning took place after about a week, thus more than one month earlier than the usual first appearance of larvae in plankton. Presumably this is due to the relatively high temperature in the culture bowls.

Size and general characteristics of the pelagic larva

Stage	Length mm	Width mm
Trochophore	0.12	0.08
1 segment	0.16	0.08
2 ,, ...	0.19–0.24	0.10
21 ,, ...	1.70	0.18
25 ,, ...	2.25–2.50	0.20

This species is the only one of the genus which has black eyes.

The unsegmented trochophore (fig. 12a)

The unsegmented trochophore is opaque milkish white due to its abundant yolk. It is surrounded by the finely sculptured egg-membrane. Somewhat anterior of the middle there is a continuous uniserial prototroch. On the ventral side the slit-like blastopore is noticeable. Eyes are lacking.

The trochophore with an indicated segmentation

This stage is attained about 24 hours later. The prostomium has acquired a small weak apical tuft and a pair of black eyes. The prototroch is no

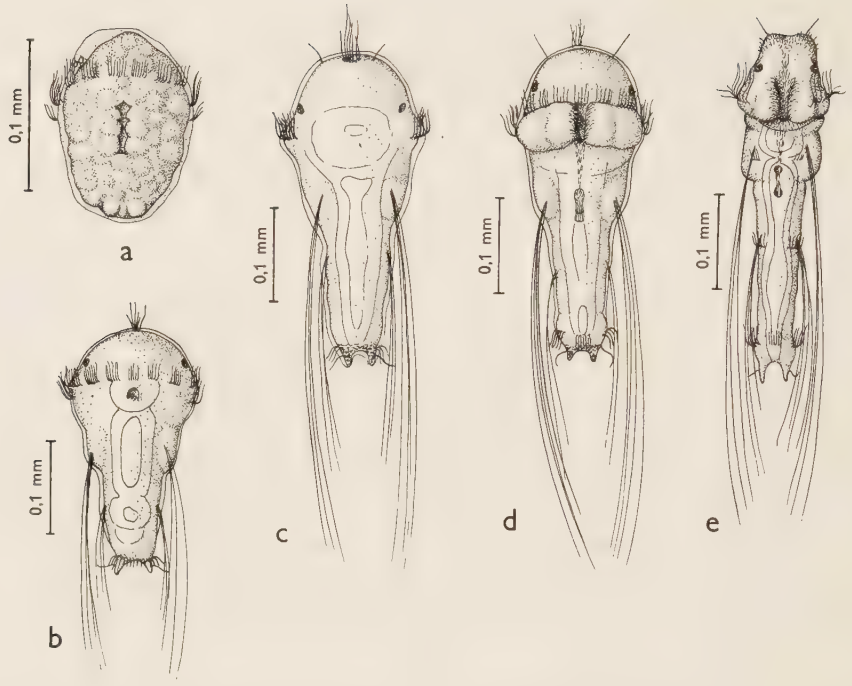


Fig. 12. *Prionospio malmgreni* Claparède. a) Trochophore (ventral view). b) Young 2-segment stage (ventral view). c) and d) Somewhat older 2-segment stage (dorsal and ventral view). e) Late 2-segment stage (ventral view).

longer dorsally continuous, a wide gap has been formed here. A second row of ciliated cells in the prototroch is formed laterally, posterior to the first. In the middle section of the body there is an indication of a pair of setae sacs, and anlages to two larval bristles are observed on either side. A pygidium with two cirri, each with a stiff, distally directed cilia, and a telotroch has also appeared. It is discrenible that the digestive apparatous consists of three parts.

The larva with one complete segment and the indication of a second (fig. 12 b–d)

After another 48 hours the larva has a first segment with large setae sacs and additional anlages to still another pair. The larval setae in the first segment are long and extend somewhat posterior to the pygidium. In the second segment they are somewhat shorter. The apical tuft has increased in length and size. There is still only one pair of eyes. The ventral side of the ciliae row of the prototroch is still continuous, although the dorsal is discontinuous. The lateral posterior ciliated cells have become larger. The blastopore is closed and were it had its anterior end there is an anlage to the mouth. Three divisions of the digestive apparatus are

discernible whose lumina do not communicate. In this stage there exist still no traces of the vestibule and lateral lips. The peristomium is, however, somewhat thickened were the latter will be formed later on. There are no indications of a "ciliated pit", of gastrotrochs, and of a neurotroch. After another 10 hours, however, anlages to the lateral lips begin to swell up on both sides of the mouth opening (fig. 12d) which now lies at the bottom of a slit-like vestibule. The anterior row of prototrochal cells is still present and ventrally continous. Its ventral part lies immediately anterior to the anlages of the lateral lips. A neurotroch runs posteriorly from the vestibule and ends in a "ciliated pit". The prostomium has acquired a pair of tactile ciliae. The connection between the oesophagus and the stomach is still closed but the stomach and the rectum appear to communicate with each other (fig. 12c).

The late 2-segment stage (fig. 12e)

After another 24 hours the prostomium has been considerably stretched. The apical tuft has disappeared but the tactile cilia still remain. The anterior row (i.e., the first formed) in the prototroch has dissappeared and the posterior has developed strongly. The lateral lips now have essentially the same form as in the larva ready to metamorphose, and are finely ciliated on the inside. On the upper side of the prostomium another pair of eyes is found, medial to the first ones. These are also black. The body has undergone considerable extension and has become thinner in relation to the length. The "ciliated pit" has grown and its ciliation has become stronger. On either side of this there is a pair of small ciliated cells. In segment 2 the first gastrotroch is observed. Its ciliated cells are laterally placed. The dividing wall between the oesophagus and stomach is still in its place. The larva has thus not begun to ingest any food. On the pygidium, which has been somewhat stretched, a brownish yellow pigment has been formed. Larvae of this stage have also been obtained in plankton. The observations on the cultured larvae were discontinued here. Some specimens could be reared up to the 20-segment stage.

The larva ready to metamorphose (figs. 13a–b)

The following description is based mainly upon two individuals from plankton: one with 24 segments and a length of 2.40 mm, and the other with 24 segments and a length of 2.25 mm.

The prostomium has acquired in its posterior part a crest which extends posteriorly. The medial eyes have taken on the form of apple seeds, the lateral ones are more elongated in dorsal view. There is a pair of very short palpi. Weak, dorsal, parapodial cirri are found in all segments except in the first. Ventral parapodial cirri are found in the segments 2 and 3.

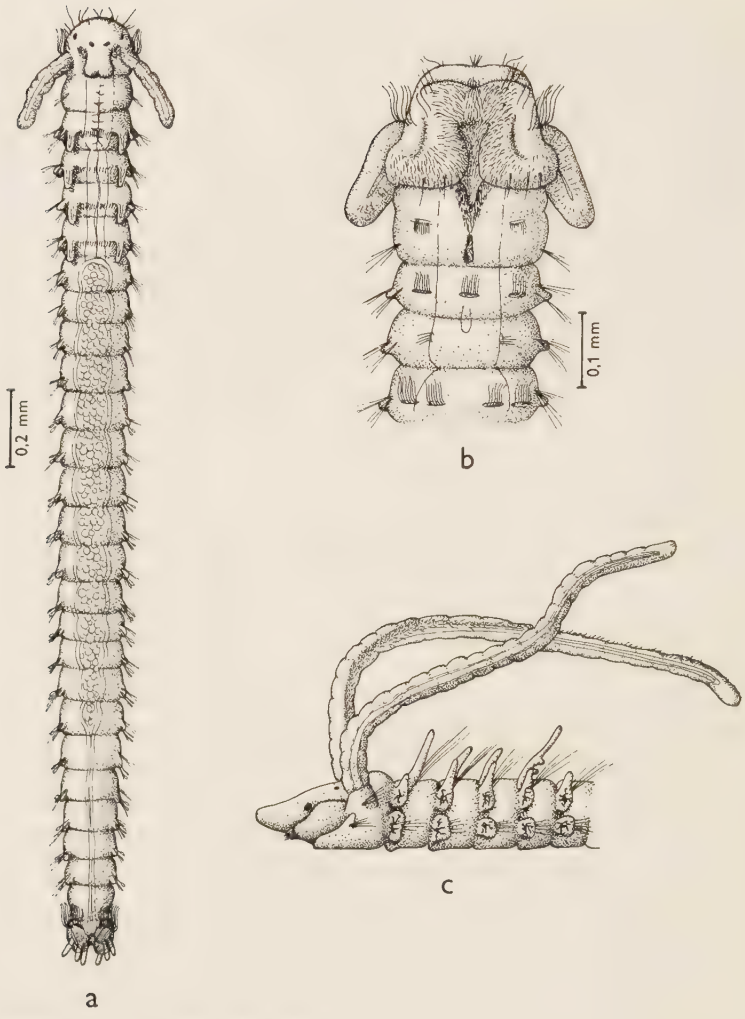


Fig. 13. *Prionospio malmgreni* Claparède a) and b) Pelagic larva ready to metamorphose. Larval setae shed. a) Dorsal view. b) Fore-part, ventral view. c) Bottom stage with 30 segments 14 days after metamorphosis. Fore-part (lateral view).

Segment 1 is considerably longer than the succeeding ones. Branchial anlages occur in segments 2–5. Nototrochs are lacking in all segments except those bearing branchiae. The pygidium is richly provided with bacillary glands (see p. 171) and has three pairs of cirri of about the same size (fig. 13a). The dorsal pigmentation is exceedingly weak except on the pygidium, and is composed of diffusely scattered melanin granules. The pygidium exhibits the previously mentioned yellowish-brown pigment. The pharynx extends through segment 2, the oesophagus through segment 5, and the

stomach through segment 18. The rectum is straight. Of adult bristles there are both dorsal and ventral hairy bristles as well as dorsal and ventral hooded crochets. The ventral hooded crochets begin in segment 10 and the dorsal in segment 22 or 23. The "ciliated pit" and the neurotroch have not undergone any essential change since the 2-segment stage. The first gastrotroch, i.e. the one in segment 2, has acquired an additional ciliated cell which is medially located. In the next segment there is only one pair of ciliated cells. In the subsequent segments there are four ciliated cells in the gastrotrochs.

The young benthonic stage (fig. 13c)

The following description is based upon two individuals, which metamorphosed in mud from their natural biotope and were examined about 14 days after the metamorphosis. One specimen had 30 segments, a length of 3.4 mm and a width of 0.16 mm; the other specimen was somewhat smaller (28 segments).

The prostomium has been lengthened and flattened. Terminally it is truncate, posteriorly it comes to an end in a crest, which is considerably higher and narrower than in the larva, but insignificantly longer. The nuchal organs have become larger. The eyes are unaltered. The palpi have increased greatly in length and are very narrow. In the first segment a pair of longitudinal folds have been formed dorsally, which border the nuchal organs laterally. There are both dorsal and ventral cirri in segment 1, but they are relatively insignificant. In the following segments the ventral cirri are leaf-shaped and rounded, and the dorsal leaf-shaped, long and tapered, and decrease rapidly in length posteriorly. Four pairs of branchiae are found from segment 2. In segments 2 and 5 they are longer than in the intermediate segments. The most posterior pair is provided with small processes, which give them the shapes of combs. The dorsal cirri in segment 7 have fused with a transversal integumental fold. The pygidium is pigmented yellowish-brown and bears a large median cirrus and a pair of shorter lateral ones. A reduction of the number of cirri and a displacement of one cirrus has thus taken place. As in the larva ready to metamorphose ventral hooded crochets are found from segment 10 and dorsal ones from segment 23 onwards. They are of the same type as in the sexually mature worm.

Biology of the benthonic stage

The worm builds very thin, hyaline tubes which are not very permanent. They are profusely branched. The benthonic stage seems to live on detritus.

Literature

Fewkes (1883) described a larva which he classified as *Prionospio tenuis*. Giard (1886) and Cerruti (1911) pointed out that Fewkes' larva must belong to *Magellona papillicornis*. Lo Bianco (1899) has reported that the species in the Mediterranean Sea spawn in June and July, and that he obtained larvae which metamorphosed into *Prionospio*. He neither described nor figured them. Cerruti (op. cit.) has given a very incomplete description of the larva but has not figured it. Gravely (1909 A) reproduced and described a larva which he designated as "*Spionid A*". Since his account concerns only the anterior part it is very difficult to draw any definite conclusions regarding the identity of the species, although there is much in favour of its being a *Prionospio* larva. Later he dealt once more with this larva (1909 B, p. 38, pl. 3, figs. 33–34). Several of its now described characteristics, e.g., the occurrence of ventral hooded crochets from segment 10 onwards, the form of the prostomium, and the long narrow body, support the view that it is a *Prionospio* larva. Finally, Thorson (1946, pp. 102–103, figs. 55 A–B) described a larva, provisionally classified by him as *Disoma multisetosum*, which certainly ought to be referred to this species. This is borne out by the body form, the weak larval setae, and the colour of the eyes. The larva of *Disoma multisetosum* has been described on page 141 in this paper.) Fage and Legendre (1927) showed that the sexually mature animal swims freely on the surface during night, which can indicate that the species has an epitoquous spawning.

Prionospio steenstrupi Malmgren

Occurrence in the area of investigation

The species occurs in the Gullmar Fjord and has the same depth range as the foregoing, but is considerably less numerous.

The egg

The egg is oval (180 μ, 120 μ) and yellowish red in colour. The egg membrane is thick, with membrane vesicles scattered over it.

Occurrence in plankton

The larva has been obtained from the middle of March until the middle of May. It reaches its maximum at the end of March, when at times it can dominate the annelid plankton.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
2	0.26	0.12
6	0.60	0.12
12	0.90	0.18
21	1.70	0.20

This larva diverges from the other *Prionospio* larvae in that it has red pigment dorsally.

The larva ready to metamorphose (figs. 14b–d)

For the discription a specimen with 19 segments has been selected. (The figured larvae are younger stages, but they agree in essential parts with the one described.)

There are two pairs of red eyes. The median eye are oval and transversely orientated. The lateral ones are rounded. Palpi are lacking. The nuchal organs are relatively narrow and located on either side of a broad nuchal crest. Nototrochs are lacking. Segment 1 is considerably more developed than the succeeding ones. The parapodia are very slightly differentiated. Branchial anlages are lacking. There are three pairs of cirri in the pygidium (a larva with 7 segments has one pair, one with 9 segments two pairs). Along the entire dorsal side of the larva there is a diffusely scattered beautiful red pigmentation, which is characteristic of this species. It is accentuated at the "neck" and at the pygidium. The oesophagus extends through segment 1, where it is followed by a stomach, which in turn merges into a convoluted rectum. The larval setae are somewhat longer than in the foregoing species. Of adult bristles there are both dorsal and ventral hairy bristles in all segments as well as dorsal and ventral hooded crochets in the hind segments. The ventral hooded crochets occur from segment 9, and the dorsal from segment 13 onwards. In the ventral parts of the prototroch there are several tactile cilia interspersed. The "ciliated pit" complex in this species is more complicated than in any other species which I have examined. The neurotroch is broad in its anterior part but narrows rapidly towards the "ciliated pit", which is located in segment 1. It forms a distinct depression, which is limited posteriorly by a ciliated cell directed transversally to the body. On either side of the "ciliated pit" there are three stiff cilia which are medially directed. The movements of these cilia are slow and pendulous. Beyond these there is on either side another ciliated cell which is longitudinally directed. Posterior to the median group of cilia there follows in segment 2 an oval, ciliated, somewhat depressed region,

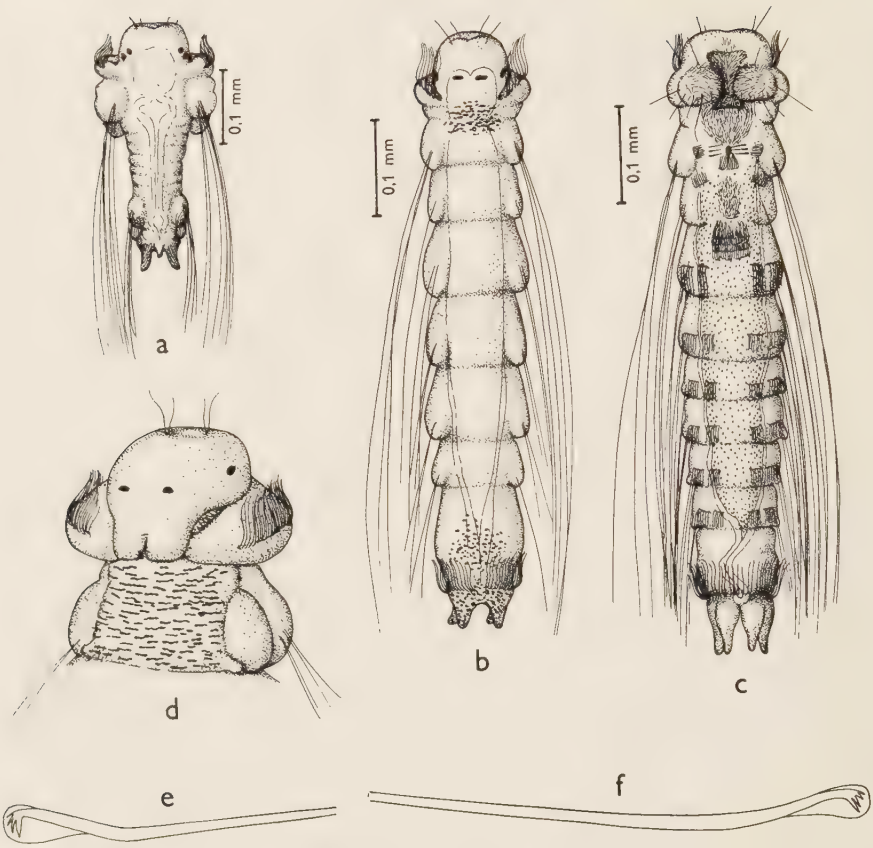


Fig. 14. *Prionospio steenstrupi* Malmgren. a) 2-segment stage presumably belonging to this species (dorsal view). b) 8-segment stage (dorsal view). c) 8-segment stage (ventral view). d) 21-segment stage. Fore-part seen obliquely from above. Larval setae shed. e) Ventral hooded crochet from young bottom stage. f) Dorsal hooded crochet from the same.

where the cilia appear to be immobile and irregularly arranged. On either side of this "oval" there occurs in the anterior part of the segment a pair of ciliated cells which are diagonally directed. Finally, in the third segment there is a region with relatively long cilia, which are arranged in several rows, one after the other. These are immobile and directed longitudinally to the body. On either side of this ciliated region is located the first gastrotroch, which is considerably more developed than in the following segments. The gastrotrochs consist of four ciliated cells each, which are situated two by two, laterally in the segment.

The young benthonic stage

Also these larvae are very difficult to get to metamorphose in culture bowls. The two animals, which form the basis of the following description both had 19 segments and a length of 1.40 and 1.74 mm respectively.

The prostomium, the peristomium and the eyes have not undergone any changes. The nuchal organs have increased into a pair of transversely placed ciliated ovals. The palpi have grown considerably. In the larger specimen they reached beyond segment 5 when posteriorly directed. The parapodia in segment 1 are insignificant. In the following segments the dorsal and ventral cirri are well developed with their most noticeable development in the anterior part of the body. The dorsal cirri are longest in segment 3, where they are leaf-shaped and tapered. Only one pair of branchiae, viz. in segment 3, occurs. The branchiae are well separated from the dorsal cirri. The pygidium has developed in the same manner as in *Prionospio malmgreni* (p. 45). The oesophagus extends through segment 3 and the stomach through segment 15. The rectum is convoluted. The red pigment in the "neck" has been concentrated. Otherwise the pigmentation is the same as in the larva. There are dorsal and ventral hairy bristles in all segments. Ventral hooded crochets are found from segment 10 (fig. 14e), and dorsal from segment 14 (fig. 14f) onwards.

Identity of species

Since I did not succeed in rearing cultures so far that unmistakeable adult characteristics were developed the identity of the species is somewhat uncertain. The larva can, nevertheless, undoubtedly be referred to *Prionospio*, as it exhibits a series of characteristics which are common to larvae whose species has been definitely established. Otherwise the dorsal and ventral multiserrated hooded crochets favour this view. Since in addition to *P. malmgreni* and *P. cirrifera* also *P. steenstrupi* occurs in the area of investigation and no other larva, which can reasonably be referred to this genus except the larvae of the two first-mentioned species, have been observed, this larva should with fairly great certainty be classified as belonging to the last-mentioned. This is also supported by the form of the hooded crochets.

Literature

Söderström (1920) has incorrectly stated that the egg is provided with only one, yet large membrane vesicle.

Prionospio cirrifera Wirén

Occurrence in the area of investigation

The species has about the same depth range as the two foregoing species and is a pronounced mud-bottom form.

Occurrence in plankton

The larva is encountered during the same period as *P. malmgreni*, i.e. during the middle and later part of the summer. It has been observed earliest on July 7 (1948) and latest on September 5 (1952).

Size and general characteristics of the larva

The size agrees with that of *P. malmgreni*. The larva is, however, slightly thicker and more robust than the latter, from which it otherwise differs mainly in the colour of the eyes. It is distinguished from *P. steenstrupi* among other things by the absence of red pigment dorsally.

The larva ready to metamorphose

As typical of the stage a larva with 19 segments has been chosen.

The rounded prostomium is provided with two pairs of tactile cilia. The posterior margin of the nuchal crest is stumpy. The palpi are considerably more robust than in larvae of the two other *Prionospio* species. They bear a ciliation, which I have not observed in any other spionid larva. Thus they have no uniformly ciliated groove, but the ciliation is divided up into well separated ciliated cells as on the branchiae. The nuchal organs are large and oval. Segment 1 lacks appendages and is much larger than the succeeding segments. The following parapodia are considerably further developed than in the larvae of the other *Prionospio* species. Branchiae are found in segments 2 4. The nototrochs are insignificant and occur only in the same segments as the branchiae. The pygidium, which is pigmented yellowish-brown, bears four anal cirri. The telotroch is relatively weak. With the exception of the pygidium and the eye spots the larva is completely unpigmented. The pharynx, which extends to about the middle of segment 2, often has on the inside a reddish-brown pigmentation. The most anterior part of the stomach has a weak bluish pigmentation and its walls often contain oil drops. It is most frequently provided with yellowish-green contents. A rectum is discerned. The larval setae are generically typical (p. 40). Dorsal and ventral hairy bristles are found. Ventral hooded crochets occur from segment 10 onwards and are multiserrated. The dorsal appear first farther caudad but are of the same type. In the fine ciliation of the vestibule there is a number of longer tactile cilia. On the inside of the lateral lips of the vestibule there is a pair of soft processes, which I have not observed in any other Spionid larva (fig. 15b). The ventral lip has a deep slit medially. The aperture of the vestibule thus acquires a cross-shaped appearance. A "ciliated pit" is located in segments 2–3. The neurotroch is surrounded in segment 1 by a pair of large ciliated cells. Posterior to the "ciliated pit" is a number of long cilia.

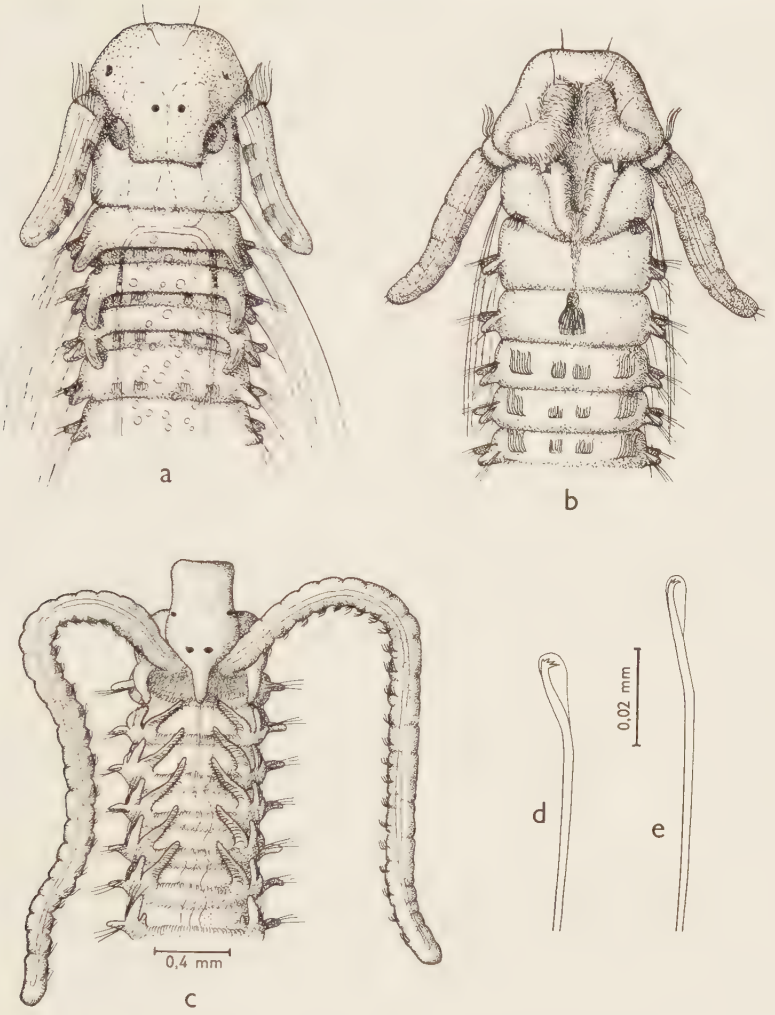


Fig. 15. *Prionospio cirrifera* Wirén. a) Pelagic larva ready to metamorphose. Fore-part (dorsal view). b) Pelagic larva ready to metamorphose (somewhat older stage than in a). Fore-part (ventral view). c) Bottom stage 14 days after metamorphosis. Fore-part (dorsal view). d) Ventral hooded crochet from a young bottom stage. e) Dorsal hooded crochet from the same.

Gastrotrochs occur from segment 4 onwards. Thereafter they appear in all segments and consist of four ciliated cells each. The lateral cilia are longer than the median.

The young benthonic stage (figs. 15c–e)

On some occasions I have been successful in getting a small number of these larvae to metamorphose. Some individuals were examined about 14 days after the metamorphosis. In this stage the prostomium has been

considerably stretched, and is now about twice as long as it is wide and truncate at the tip. The nuchal crest has grown through segment 1. The palpi are long and when drawn back reach beyond segment 12. Their peculiar ciliation is unaltered (cf. p. 50). The eyes are unchanged. The nuchal organs have increased in size, but are of the same type as in the pelagic larva. The first setiger is provided with both dorsal and ventral cirri. The dorsal ones have been largely transformed into longitudinal folds, which, as in *P. Malmgreni*, limit the nuchal organs laterally. Both dorsal and ventral hairy bristles are found in all segments. From segment 2 onwards the ventral cirri are oval and well developed. The dorsal cirri are tapered, longest in segment 3, and thereafter decrease in size. Five pairs of branchiae with the indication of a sixth are found from segment 2 onwards. They are tapered, ciliated, and lacking in all appendages. Nototrochs are found in all branchial segments. The permanent bristles are the same as in the larva. The pygidium has developed in the same manner as in *P. malmgreni*.

Two and a half months after the metamorphosis some individuals were examined, of which the largest had 58 segments. It did not differ essentially from the described stage but had eight pairs of branchiae.

Identity of species

The number and formation of the branchiae, the appearance of the hooded crochets, etc. exclude every other species except *P. cirrifera*.

Literature

The development of the species has not been treated earlier.

Fage and Legendre (1927) obtained sexually mature individuals in night-plankton, which indicates an epitoquous spawning.

Scolelepis Blainville (sensu Mesnil)

The egg and sperm

The egg is somewhat flattened and has a thick membrane and vesicles. The sperm is short-headed.

Type of development

The development is largely pelagic and predominantly planktotrophic.

The pelagic larva

The larvae are short and thick in relation to their length. The latter does not exceed 1 mm. The prostomium is broad and somewhat notched

terminally. The lateral parts of the peristomium are very clearly demarcated from the prostomium. The palpi are attached far out on the lateral parts of the peristomium and remain relatively short. The nuchal organs are groove-shaped and longitudinal. There are three pairs of black eyes. The lateral pair are double eyes (se p. 155). A broad and stumpy nuchal crest is observable. The parapodia are strongly differentiated. Branchial anlages are lacking. Nototrochs may occur but are weak. The pygidium is large and rounded, and acquires dorsal cirri. Gastrotrochs do *not* occur in every segment caudad of the "ciliated pit". This is located in segment 2. The larval setae are short, strong, and somewhat curved. The pigmentation is vivid.

Key to species

1. Yellow pigment completely lacking. The peristomium is richly pigmented black. *Scolelepis girardi* (p. 58). 1.
   Yellow pigment occurs. The prostomium is not or only slightly dark pigmented. 2.
2. Dorsal yellow pigment spots from segment 2 onwards. The ventral cirri in segment 3 are considerably larger than in segment 2. *Scolelepis fuliginosa* (p. 57).
3. No dorsal yellow pigment spots. The ventral cirri in segment 3 are not appreciably larger than in segment 2. *Scolelepis ciliata* (p. 53).

Scolelepis ciliata (Keferstein)

Occurrence in the area of investigation

The species is very common on sand bottoms in not too surf-exposed places. In the bay of Kristineberg it is found from the water-line down to a depth of about 2 m. There it can be exceedingly numerous during certain periods. This is specially the case immediately after the settlement of larvae in the autumn.

The egg and sperm

The egg is oval and somewhat flattened whith a length of 0.15 mm and a width of 0.10 mm. There are 18–22 membrane vesicles. The colour is yellowish gray. The sperm is of the short-headed type.

Occurrence in plankton

The larva occurs in plankton during the middle and later part of the summer. It has been observed earliest on June 21 (1948) and latest on September 10 (1951). It occurs in greatest numbers in July.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
3	0.28	0.12
6	0.43	0.14
10	0.70	0.24
12	0.84	0.24

The similarities to and differences from the larva of *S. fuliginosa* are given elsewhere (p. 58).

The larva ready to metamorphose (figs. 16 c–d)

A 11-segment stage is described. The prostomium bears a pair of lateral processes, which are provided with ciliae. Posteriorly the prostomium forms a very broad crest, which reaches to the anterior boundary of segment 1. The four most medial eyes are circular; the lateral, when viewed from above, are kidney-shaped (double eyes). Groove-shaped longitudinal nuchal organs are found on either side of the crest. The parapodia are well differentiated. The length of the cirri increases towards the middle section of the body, and then decreases. Nototrochs are found from segment 2 and onwards consist of five cells each. The prostomium has a yellowish-green pigmentation. Ventral to the proximal parts of the palpi there is a pair of large chromatophores which are yellowish-white in reflected light. Segments 1 and 2 are almost colourless. The rest of the body has a chocolate-brown pigmentation which is most pronounced along the median line. Towards the pygidium this concentration of pigment narrows to a tip. The pygidium is dorsally pigmented brown with darker pigment near the base of the very robust telotroch. One or two yellowish-white (reflected light) chromatophores may occur ventrally on the pygidium. The inside of the pharynx is often, but not always, pigmented black. The brown pigmented stomach merges without any demarcation into a narrowing part, which runs into the anus. Of adult bristles there are both hairy bristles, and ventral hooded crochets. The latter are found from segment 8 onwards in a number of 1 4 per neuropodium. The neurotroch is surrounded on the border between the peristomium and segment 1 by a pair of large ciliated cells, and farther caudad by two pairs located in segm. 1. The "ciliated pit" is markedly developed, located in segment 2, and surrounded by a pair of ciliated cells. Gastrotrochs occur in alternate segments beginning with the third, and consist of four ciliated cells each. The cilia in the medial cells are shorter than in the lateral. Ventrally there is also a chocolate-brown pigmentation which is lacking in segments 1 and 2 only.

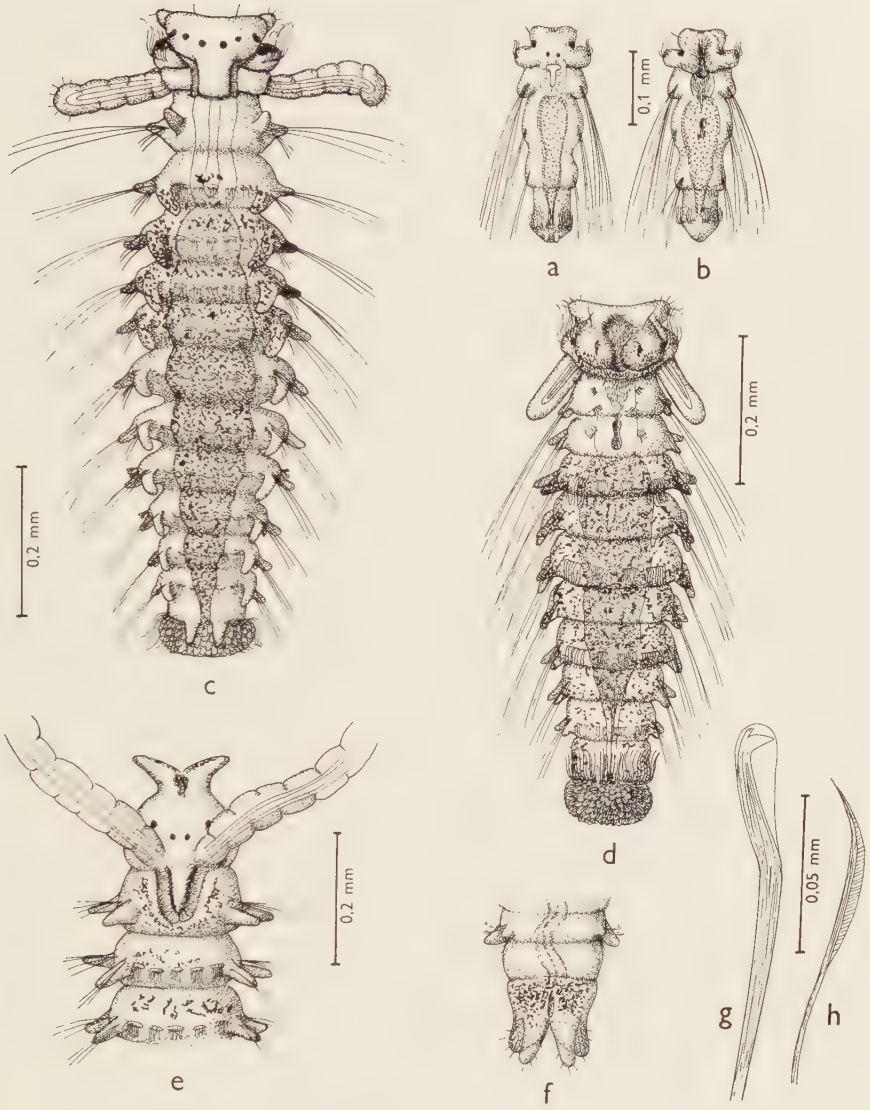


Fig. 16. *Scolelepis ciliata* (Keferstein). a) and b) Dorsal and ventral view of a pelagic 3-segment stage. c) Pelagic larva ready to metamorphose (dorsal view). d) Pelagic larva. Somewhat younger stage than in a. (Ventral view). e) Young bottom stage with 17 segments. Fore part (dorsal view). f) Hind-part of the same (dorsal view). g) Ventral hooded crochet from the same. h) Ventral "winged" bristle from the same.

The young benthonic stage (figs. 16e–h)

After the metamorphosis the changes take place very rapidly. One individual which was examined one week after metamorphosis had 17 setigers, and a length of 1.66 mm. The lateral processes of the prostomium have

grown markedly. The entire body and especially the palpi have undergone a very pronounced elongation. The pair of eyes next to the medial pair has been reduced. The parapodia have been stretched somewhat farther; branchiae are still lacking. The pigmentation is unchanged. The pharynx retains its dark pigmentation and extends through segment 2. An oesophagus has been differentiated and extends to about segment 4 or 5, where it merges into the stomach which, in turn, runs into a convoluted rectum. No alterations have occurred regarding the adult bristles.

A one-month-old specimen had 17 segments and a length of 4.56 mm. The lateral processes of the prostomium have grown somewhat. The nuchal organs have increased in size and acquired the typical "horseshoe" shape of the genus. The parapodia have developed a pronounced leaf-shape. The dorsal cirri, at least in the anterior part of the body, are round-tipped. At this stage branchiae have also developed, and are found from segment 2 onwards. The dorsal cirri are fused for a large part of their length with the branchiae. The nototrochs are composed of up to 12 ciliated cells. Presumably a very weak posterior row of ciliated cells has also appeared in the nototrochs. The pygidium has three pairs of cirri. The pharynx extends through segment 3, and the oesophagus through segment 10. The stomach is pigmented brown and extends through segment 24. The rectum is colourless. Ventral hooded crochets first occur here from segment 15 onwards in a number of 3–4 per neuropodium. They are accompanied in each neuropodium by a coarse straight bristle. The hooded crochets are diserrated (fig. 16g). The pigmentation is partially reduced.

After two additional months a specimen had 36 segments and a length of 3.65 mm, another 34 segments and a length of 4.00 mm, and a third 53 segments and a length of 10.2 mm. The pigmentation in these stages is totally reduced. Branchiae are also discernible in segment 1. The pygidium has three to four pairs of cirri. The ventral hooded crochets appeared in the largest specimen from segment 20 onwards, and their number had increased to four to five in each neuropodium. They were accompanied by two of the previously mentioned straight bristles.

One specimen, which was bread for three months, and which was especially richly fed (with planktonic organisms), had 72 segments and a length of 22 mm. The hooded crochets first began here from segment 27 onwards.

Identity of species

The pelagic larva much resembles that of *Scolelepis fuliginosa* (see p. 57). In the beginning I was inclined to regard the small divergencies as individual variations in *S. fuliginosa* larvae. A prolonged culture of the bottom stages has shown, however, that this is not the case.

From our faunal region three species of this genus are known, viz. *S. fu-*

liginosa, *S. ciliata*, and *S. girardi*. Of these the two first-mentioned have diserrated hooded crochets, and the last-mentioned triserrated. *S. girardi* has also a much larger number of such bristles per neuropodium, viz., up to 23. The largest of the previously described stages still had five to six hooded crochets per neuropodium, and these were diserrated. Therefore *S. Girardi* can be excluded here. The two other species resemble each other very much. One difference exists in the pigmentation. Typical of *S. fuliginosa* is a white pigmentation of the prostomium, which is always absent in *S. ciliata*. I have noted such white pigment even in very young bottom forms obtained from cultures of larvae which certainly belong to *S. fuliginosa*, but never in the young bottom forms obtained from cultures of the larvae described in the foregoing. In my opinion the strongest indication for *S. ciliata* is, however, the number of dorsal organs. In the largest bottom stage described here they occur in one pair per segment. Söderström (1920) reports this as generically characteristic of *Colobranchus*, the genus to which he considered *S. ciliata* to belong. On the other hand, *Nerine*, the genus under which he classified *S. fuliginosa*, should have two pairs per segment. These organs can be readily demonstrated by staining with iodine green, which strongly stains the mucous glands in the epidermis. Since such are lacking in the dorsal organs these will appear as lighter parts. The larva should therefore with very great probability be referred to *S. ciliata*.

Biology of the benthonic stage

This species does not build any permanent tubes. It moves freely burrowing under the surface of substratum, and sticks up its palpi where there is a good supply of food. It cleverly catches small planktonic animals, but also eats detritus.

Literature

The egg was first described by Keferstein (1862, pp. 118–120, pl. X., figs. 12–18).

Scolelepis fuliginosa (Claparède)

Occurrence in the area of investigation

The species is found at a somewhat greater depth than the foregoing. It seems to prefer bottoms with decaying *Zostera* and decaying algae at a depth of about 5–15 m.

Occurrence in plankton

The larva occurs in plankton from the beginning of July until December.

Size of the larva

The larva agrees in size with *S. ciliata.*

The pelagic larva (fig. 17d)

Since the larval development of this species is already well known, I shall not give a complete description but only point out some characteristics which distinguish it from the otherwise very similar *S. ciliata* (p. 53). The most noticeable difference lies in the pigmentation of the dorsal side. In this species there occurs in every segment from the second onwards a pair of chromatophores, which appear yellow in reflected light. These are not found in *S. ciliata.* Another obvious difference is the more robust formation of the ventral cirrus in segment 3 in this species. This is appreciably longer than in the preceding segment, and is more vividly pigmented brown than both the preceeding and succeeding ones. This is not the case in *S. ciliata.*

Literature

The development of this species is very well known. Claparède and Mecznikow (1869, pp. 169–170, Pl. XII., figs. 1 A–1 M) described the egg and the pseudocopulation that precedes the egg-laying and sperm-emission. They also described the young larva (3 segments). More recently Day (1934, pp. 633–654, figs. 1–16) has given an outstanding description of the entire larval development from the egg to the young benthonic stage. He showed that the development is wholly pelagic.

Scolelepis girardi (Quatrefages)

Occurrence in the area of investigation

The species is known from the area of investigation (Malmgren 1867). It is found in shell-gravel near the harbour of the island Bonden (G. Gustafson, verbal communication).

Occurrence in plankton

The larva has appeared very rarely in plankton from the end of April to the beginning of May. Not more than five or six larvae have been obtained.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
8	0.72	0.22

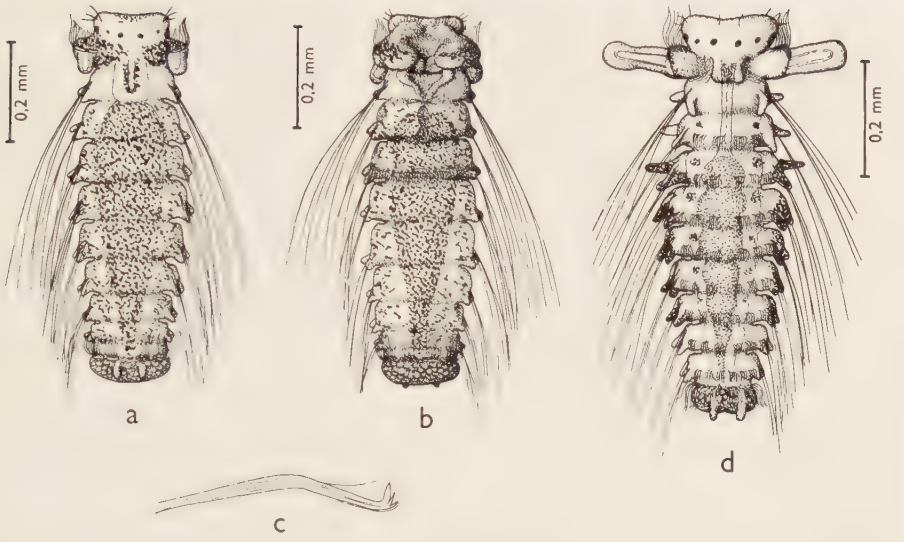


Fig. 17. *Scolelepis girardi* (Quatrefages). a) and b) Pelagic larva presumably belonging to this species (dorsal and ventral view). c) Ventral hooded crochets from this larva. *Scolelepis fuliginosa* (Claparède). d) Pelagic larva (dorsal view).

The larva greatly resembles the two foregoing species. It differs from them, however, by lacking yellow pigment, the prostomium and peristomium are strongly pigmented black, and lateral processes are not formed during the pelagic life.

The larva ready to metamorphose (figs. 17a–c)

The description is based on the previously-mentioned 8-segment stage.

The prostomium has the same appearance as that of the foregoing larvae but lateral processes are lacking. Laterally there are three pairs of tactile cilia. The indication of a nuchal organ can be discerned as a pair of ciliated grooves. The parapodia are not fully so well demarcated from the body as in the foregoing species. In segment 1 the dorsal cirri are somewhat shorter than in the following segments. Nototrochs are completely lacking. The prostomium has in its anterior part a pale yellowish-green and in its posterior lateral parts a blackish-brown pigmentation. This is most marked in the notch between the prostomium and the lateral parts of the peristomium. Such pigment is also found between the lateral parts of the peristomium and the first segment. From segment 2 onwards is found a diffuse blackish-brown pigmentation both dorsally and ventrally. Yellow pigment is completely lacking. A pharynx, with dark pigmentation on the inside, extends through segment 1. Upon this follows a brown-pigmented stomach, which opens into the anus without any distinct rectum. The anus is pig-

mented black. The prototroch runs relatively far down on the lateral lips. The neurotroch is very broad in its anterior part but then narrows rapidly. The "ciliated pit" is large and is located in segment 2 and the anterior part of segment 2. It consists of two distinctly separated parts. The anterior part is surrounded by stiff cilia. There is only one gastrotroch. It is situated in segment 3 and consists of five large, ciliated cells.

The young benthonic stage

The description is based upon one individual which metamorphosed in sand on April 30 and was examined on May 3. It had at that time 12 segments and a length of 1.08 mm.

Lateral processes on the prostomium are still lacking. The palpi are very short. The eyes show indications of incipient reduction. The median pair has almost completely disappeared. The nuchal organs have extended posteriorly and reach through segment 1. Due to the pronounced pigmentation in the "neck" it is very difficult to decide if there is a nuchal crest. Well-developed cirri occur dorsally and ventrally in all segments. The dorsal ones are round-tipped in the anterior part of the body, and acutely tipped in the posterior. Small branchial anlages can be detected in segments 3 and 4. All the ventral cirri are rounded. In the pygidium the dorsal cirri have developed further. The oesophagus extends through segment 2. A straight rectum has been differentiated. The larval pigmentation has been largely retained. Of adult bristles there are both dorsal and ventral, relatively curved, "winged" bristles in all segments, and from segment 8 onwards also ventral hooded crochets. These are triserrated (fig. 17 c).

Identity of species

The identity of the species is not quite clear. There are many strong indications, however, for classifying the larva as *S. girardi*. As the development is known for *S. fuliginosa* and *S. ciliata*, and as only one other species of this genus is found in the region, viz. *S. girardi*, it is plausible already of these grounds to refer the larva to this species. The triserrated bristles also support this classification.

Biology

The metamorphosis is induced with difficulty by clean mineral sand. The worm does not build any permanent tubes.

Literature

The development of this species has not been previously treated.

Spio Fabricius and *Microspio* Mesnil

The boundary between these two genera is obscure. Söderström (1920) showed that the basis of classification advanced by Mesnil (1896), i.e., the occurrence or absence of branchiae in segment 1, could not be accorded so great systematic value that it could differentiate the genera. He proposed instead that the occurrence of one or two pairs of dorsal organs per segment should constitute such a criterion. He showed that *Spio* had two pairs per segment, and *Microspio* but one. On the same grounds he also divided *Scolelepis* into two genera (p. 57). Later investigators (Mesnil 1925 and Fauvel 1927) have been unable to justify this division of *Scolelepis* and I share the same opinion. Consequently also here the number of dorsal organs per segment should not be considered of value for generic differentiation, and thus *Microspio* should be included in *Spio*. I have, however, not carried out this fusion, as I consider further investigation necessary. I have found, namely, that one of the examined larvae, *Microspio atlantica*, differs from the others in a few interesting points. In this larva the palpi are more developed than in the other species of the two genera, and at the bases of the palpi peculiar formations occur which are not found elsewhere; further the gastrotrochs are partially reduced, and the first pair of branchiae are first developed in segment 3, but in segment 2 in the other species. It is conceivable that *Microspio atlantica* differs so greatly in other respects from the other species that its reference to a special genus might be justified. A future anatomic investigation may decide this question.

The egg, sperm, and fertilization

The egg is of the thin-shelled type, and membrane vesicles are lacking. The sperms are long-headed and can be amalgamated in the epitoquous nephridia of the male into spermatophores. The fertilization is then probably preceded by a copulation when the spermatophores are introduced into the receptacula seminis of the female.

Type of development

The eggs are emitted to jelly-like egg masses or egg-capsules, which are stored for the most part in the tube of the female (brood protection). The larvae leave their protective convering at varying stages. Adelphophagia occurs (see pp.149–150).

The pelagic larva

The prostomium is stumpy and somewhat notched at the tip. The lateral parts of the peristomium are usually weakly demarcated from the prosto-

mium. There are three pairs of black eyes. The lateral pair are double eyes (see p. 155). Longitudinal groove-shaped nuchal organs are formed. Nototrochs occur from segment 2 onwards. The parapodia are differentiated in a relatively high degree. The larval setae are thin. The "ciliated pit" is located in segment 2. Gastrotrochs are found in alternate segments from the third onwards.

Key to species

1. Light yellow pigment (reflected light) is found. 2.
   Light yellow pigment is lacking. 6.
2. The melanin is collected in distinct melanophores. 3.
   Abundant melanin, but not collected in distinct melanophores. A pair of narrow longitudinal pigment bands is found on the nuchal crest.
   Spio martinensis Type II (p. 78).
3. The pharynx is darkly pigmented. Melanophores are more or less branched and largest in segment 3. *Spio martinensis* Type I (p. 75).
   The pharynx is not darkly pigmented. 4.
4. Three distinct melanophores in segment 2. Small larvae. Long palpi.
   Microspio atlantica (p. 85).
   No three distinct melanophores in segment 2. 5.
5. Melanophores in the form of bands. *Spio filicornis* (p. 62).
6. Melanin almost completely lacking except in the two first segments in older larvae.
   Spio multioculata? (p. 66).
   More or less abundant black pigment. A median melanophore on the prostomium.
   Spio theeli (p. 71).

Spio filicornis (O. F. Müller)

Occurrence in the area of investigation

The species is found in pure mineral sand on the so-called Trillinge sand off the island Gäven (G. Gustafson, verbal communication).

Occurrence in plankton

The larva has been obtained as early as February 6 (1952), but occurs most numerously at the end of March. Occasional specimens may be found until the end of May.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
9	0.88	0.24
13	1.26	0.24
19	1.80	0.30

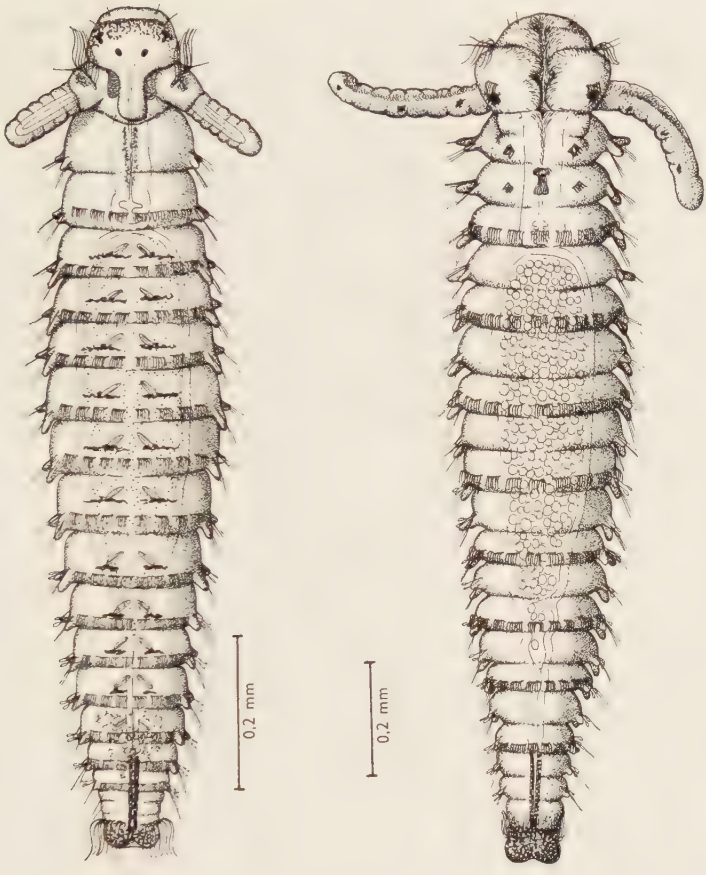


Fig. 18. *Spio filicornis* (O. F. Müller). a) and b) Pelagic larvae ready to metamorphose (dorsal and ventral view). Larval setae shed.

The larva is characterized by yellow pigment on the under side of the peristomium and pygidium, band-shaped melanophores in every segment from the third and black-pigmented proctodeum.

The 11-segment stage

The prostomium is rounded and bears a pair of groups of tactile cilia. It is weakly pigmented green. The medial eyes are round. The two lateral pairs coincide when viewed from above. The prototroch is relatively well developed. The palpi are short, only about 1 segment in length, and are attached to a pair of structures which in turn are attached to the lateral parts of the peristomium. These may presumably be regarded as palpophores. Ventral to their proximal parts there is a pair of yellowish white

(reflected light) chromatophores on the peristomium. Nuchal organs have been formed. The pygidium is rounded and lacks appendages. On its ventral side there is often a yellowish white (reflected light) chromatophore. Ventral and dorsal cirri are found in segments 2–9. The dorsal cirri bear at the tip a stiff and rather long hair. Branchial anlages are lacking. Nototrochs and "grasping cilia" are not found. Along the dorsal side of the larvae there are two rows of obliquely placed "bacillary glands". From segment 3 onwards there are also two rows of band-shaped melanophores. The pharynx extends through segment 2 and exhibits a weak dark pigmentation. The wall of the stomach contains abundant oil drops. It narrows continuously towards the pygidium and is pigmented black in its most posterior part. Gastrotrochs are found in alternate segments from the third onwards. The larval setae are relatively long and in reflected light iridescent. Of adult bristles there exist only hairy bristles.

The larva ready to metamorphose (figs. 18a, b)

As types of this stage a larva with 15 segments, and one with 19 are described.

The palpi when posteriorly directed in the larger larva reach through segment 5. In some individuals they are provided with small yellow (reflected light) chromatophores. The parapodial cirri have grown considerably. "Bacillary glands" are found in the dorsal cirri from segment 3 onwards. Dorsal and ventral hairy bristles occur in all segments except segment 1, where the dorsal ones are lacking. Ventral diserrated hooded crochets occur from segment 9. Dorsally nototrochs have appeared. The larval setae are easily discarded in this stage.

The young benthonic stage (fig. 19)

The description is based on a 16-segment stage.

The prostomium is extended forwards and round-tipped. The next most medial pair of eyes is undergoing reduction. The palpi have grown appreciably and are provided with yellow (reflected light) chromatophores. The nuchal organ has increased in growth and extends to the boundary between segments 1 and 2. The branchiae have also appeared in segment 1 but are still very insignificant here. Otherwise the changes in the parapodia are slight. The pygidium has acquired another pair of cirri. The dorsal ones are long and unpigmented, the ventral short, broad, and pigmented brown. The larval pigmentation is partially retained. A brown pigmentation in the "neck" has appeared. In older stages this becomes more intensive. The oesophagus extends through segment 5. The alimentary canal is otherwise unchanged. The adult bristles are the same as in the 19-segment larva.

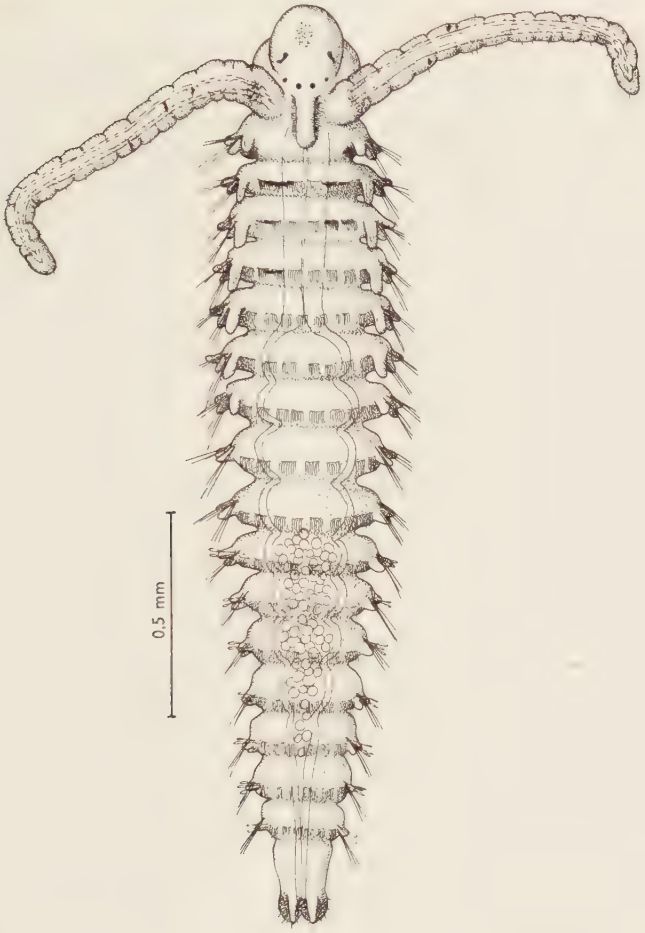


Fig. 19. *Spio filicornis* (O. F. Müller). Young bottom stage (dorsal view).

Dorsal hairy bristles are thus still lacking in segment 1. The ventral crochets are accompanied by specifically typical acicula-like, somewhat curved bristles, and begin first in segment 10.

Identity of species

The following facts speak in favour of referring the larva to *Spio filicornis:*

1. Branchiae are found from segment 1.
2. The pygidium and nuchal organs are generically typical.
3. The ventral crochets are diserrated and accompanied by aciculalike bristles. Both these bristle are specifically typical.
4. The ventral crochets occur from segment 10 onwards.

Literature

Söderström's (1920) measure of combining *Spio filicornis* and *Spio martinensis* into one species has led to a series of confusions and misunderstandings. Thus the biology of reproduction described by Mesnil and Caullery (1917, 1924) for *Spio martinensis* has been accepted as valid for *Spio filicornis*. The report by Fauvel (1927) that young specimens of this species have triserrated crochets is likewise due to this confusion.

Thorson (1946) obtained in a so-called "Mortensens detritus sampler" near Scoresby Sound, East Greenland, a young bottom stage which agrees remarkably well with a similar one I have examined. The early development of the species has been treated by Okuda (1946). He found that the egg was laid in ellipsoidal egg masses, held together by a jelly-like substance. They were attached to the bottom substratum by a stalk. The egg masses were 10–13 mm long and 5–6 mm wide; the stalk was 22 mm long and 1.5 mm thick. The eggs were 300 μ long and 200 μ wide. They were rich in yolk, brownish-green, and had a thin egg-membrane (to judge from the illustrations). The eggs developed in these jelly masses, and after about seven days the larvae left them in the 3-segment stage. Okuda followed such larvae up to the 4-segment stage. The larger larvae which he obtained in plankton, and which he considered as belonging to the species, do not agree with the pelagic larvae I have observed here. They give a strong impression of being *Nerine* larvae, which is supported by, amongst other things, the form of the prostomium.

Spio multioculata (Rioja)?

Occurrence in the area of investigation

The adult animal has not been encountered in the area of investigation.

Occurrence in plankton

The larva is encountered in plankton from the beginning of February until the end of March, and at times exceedingly abundant.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
3	0.38	0.14
5	0.50	0.16
8	0.72	0.20
11	1.11	0.20
18	1.80	0.36

This larva is characterized chiefly by the slight dorsal pigmentation, the reddish-brown pharynx, and the darkly pigmented rectum near anus.

The 3-segment stage (fig. 20a)

This is the smallest stage which has been encountered.

The prostomium is anteriorly rounded and provided with a number of tactile cilia. There are three pairs of black eyes. The lateral ones coincide when seen from above. The nuchal organs have already been formed. The parapodia are very slightly differentiated. Prototroch and telotroch are well developed but nototrochs, gastrotrochs and intersegmental ciliation are lacking. "Grasping ciliae" (p. 161) are located dorsally in the posterior segments. The "ciliated pit" has been formed. The larvae is unpigmented except in the pygidium (slight dark pigmentation), and the eyes. The pharynx extends through segment 1, followed by an unpigmented stomach. Long larval setae but no adult bristles are found.

The larva ready to metamorphose (figs. 20b–c)

The description is based on the 13-segment stage.

The prostomium has acquired terminally a slight notch. A nuchal crest has developed. The palpi are attached to short processes from the lateral parts of the peristomium (palpophores). Cirri have developed in the parapodia. The dorsal ones are very long and give the larva a characteristic appearance. They are each provided with two or three "bacillary glands" (p. 171) of the same type as found dorsally in *Spio filicornis* (p. 64) and *Spio martinensis* Type I (p. 77). Such also occur here posteriorly in each segment the second onwards. Nototrochs, which are still lacking in the 5-segment stage, are found from segment 2. The pygidium, which is amply provided with "bacillary glands", has acquired a pair of dorsal anlages to cirri. The telotroch is relatively robust. The pygidium is pigmented greenish-brown. Otherwise the larva is very slightly pigmented. The prostomium has pale yellowish-green non-structural pigmentation. There is a little, diffusely scattered melanin along the dorsal side. The pharynx is most frequently pigmented reddish-brown but can be black or blackish-brown. The stomach merges into the pygidium without any distinct rectum. Its posterior part near the pygidium is pigmented black. The under side of the prostomium is amply provided with tactile cilia. Such are also intermingled in the prototroch, which runs far down on the lateral lips. In segment 1 they are surrounded by two pairs of ciliated cells. The anterior of these is very broad. In segment 2 there is also a pair of ciliated cells on each side of the "ciliated pit". From segment 3 onwards gastrotrochs occur in alternate segments. They consist of six ciliated cells each. The larval setae are very long. Of adult bristles there occur hairy bristles, and from segment 10 onwards ventral hooded crochets.

In still older larvae (the metamorphosis can be deferred at least to the

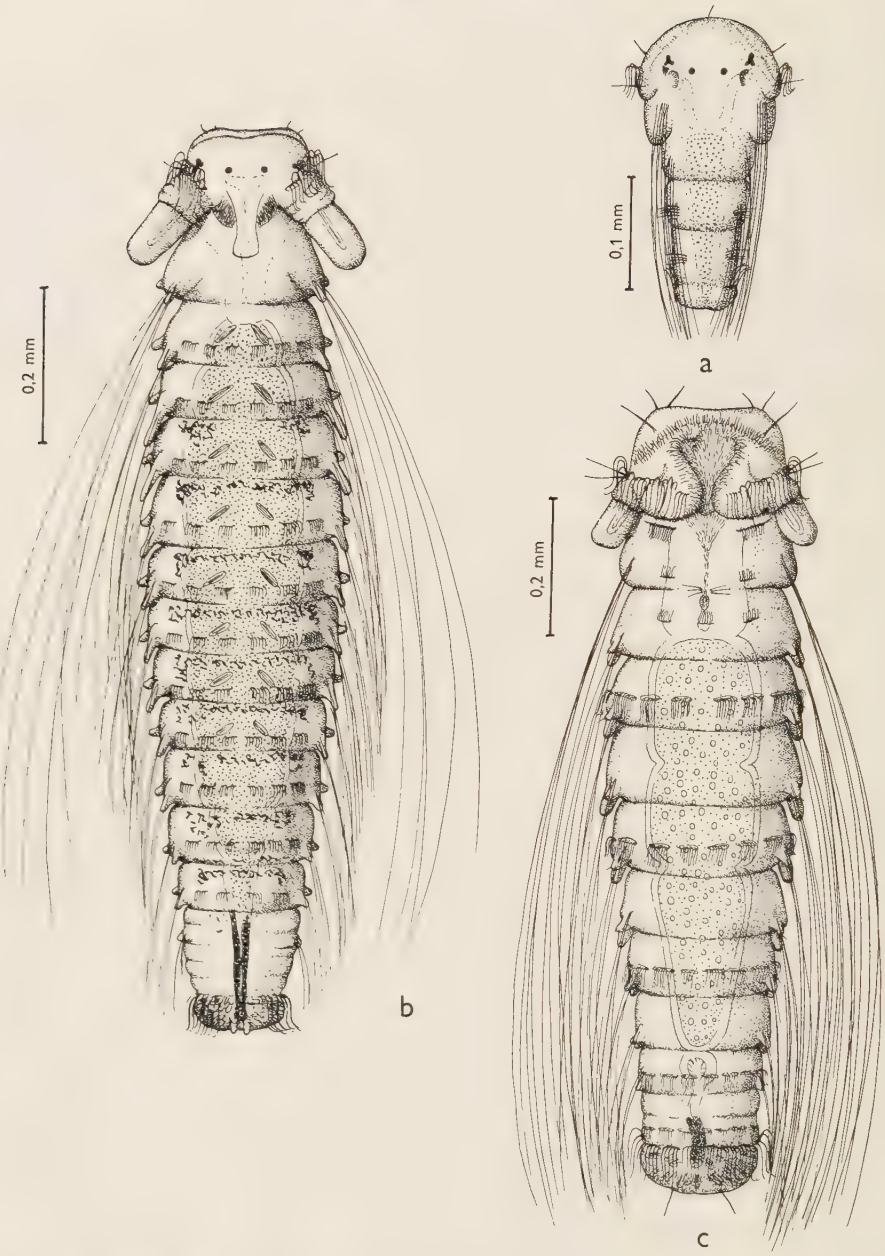


Fig. 20. *Spio multioculata* (Rioja). Pelagic larvae presumably belonging to this species. a) Youngest stage encountered (dorsal view). b) Larva ready to metamorphose (dorsal view). c) Somewhat younger larva (ventral view).

18-segment stage) branchiae are formed from segment 2 onwards. In exceptional cases anlages to branchiae are formed in segment 2 already in the 13–14-segment stage.

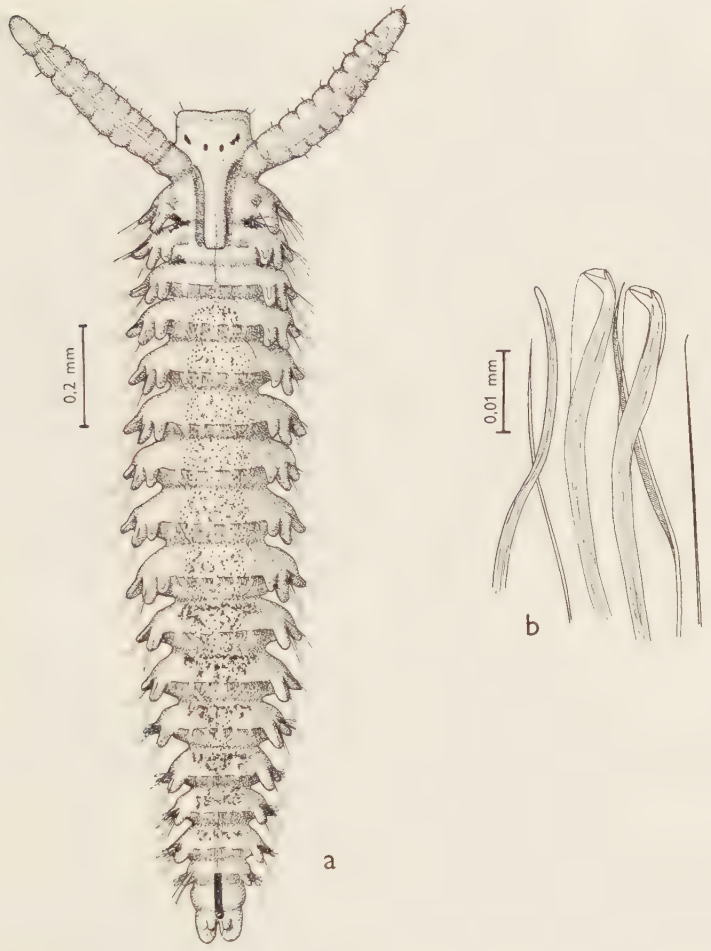


Fig. 21. *Spio multioculata* (Rioja). a) Young bottom stage (dorsal view). b) Ventral bristles from hind segment of the same.

The young benthonic stage (fig. 21)

The description is based mainly upon one individual with 16 segments and a length of 1.65 mm, and another with 45 segments and a length of 8.3 mm.

After the metamorphosis the prostomium undergoes considerable broadening. The eyes remain unaltered for a long time in certain individuals, while in others a reduction is discernible. The palpi increase greatly in length and develop yellowish white (reflected light) chromatophores. The nuchal organs first are parallel but later acquire the generically typical horseshoe appearance. Dorsal organs are formed from segment 3 onwards. It has not been ascertained whether there are one or two pairs per segment.

The parapodia are further differentiated. In segment 1 the dorsal cirrus remains insignificant. Branchiae occur first from segment 2 onwards and thereafter in every segment except in the last four or five. Nototrochs are found from segment 1 onwards. In the first two segments they are represented by only a pair of lateral ciliated cells. In the succeeding segments they are, however, complete. An intersegmental ciliation is observed. The pygidium acquires the generically typical appearance with four cirri; of these the dorsal ones are long, narrow and unpigmented while the ventral ones are short, stumpy, and pigmented brown. A melanin pigmentation occurs laterally in the anterior segments. The oesophagus extends through segment 2. Dorsal and ventral hairy bristles are found in all segments (thus also in the first). In the smaller specimen there were ventral hooded crochets from segment 10 and in the larger from segment 14 onwards. They were diserrated and accompanied by a thick acicula-like, somewhat curved bristle and hairy bristles of two types (fig. 21 b). In the larger specimen there were five to six crochets and two acicula-like bristles per neuropodium.

Identity of species

By reason of the occurrence of the gastrotrochs, formation of the pygidium, type of the nuchal organ, arrangement of the "bacillary glands", etc., the species must be sought among the genera *Spio* and *Microspio.*

Spio multioculata is indicated by the following features:

1. The form of the prostomium.
2. The form of the ventral hooded crochets.
3. The form of the acicula-like bristles.

This species is counterindicated by the following features:

1. Branchiae do not occur in segment 1.
2. The species is not observed in the area of investigation.

Regarding point 1 I have found that branchiae in the first segment develop very late in certain species belonging to this genus. This is true of, for example, *Spio martinensis,* and it is therefore conceivable that such can be the case also here. Regarding point 2 it can be said that *Spio Theeli* is not observed in the adult stage in the area but I consider that the identity of the larva as defenitely established. The identity of the species of the larva described here, however, cannot be regarded as completely determined. Possibilities that the larva belongs to a species not described previously can not be excluded.

Literature

THORSON (1946) has described a larva which he referred to *Pygospio elegans* and which he called "*large, colourless larva with short larval bristles*". It agrees remarkably well with the one described here, and they are presumably identical (se p. 98).

Spio theeli (Söderström)

Occurrence in the area of investigation

The species has not been obtained in the adult stage in the area of investigation.

Occurrence in plankton

The larva occurs from the middle of April until the end of May and is often very numerous.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
12	0.90	0.28
16	1.60	0.36
19	1.84	0.36
21	2.00	0.38

It can be difficult to distinguish the larva from that of *Spio multioculata?* which occurs during the same period in plankton. It has, however, denser dorsal pigmentation, ventral hooded crochets of another type, and no acicula-like bristles.

The 12-segment larva

The prostomium is stumpy and somewhat notched at the tip. There are three pairs of black eyes, of which the median ones are round, the lateral double-eyes, and the middle ones small. The nuchal crest of the prostomium reaches posteriorly through segment 1. The palpi are very short. Anlages to nuchal organs are formed. The parapodia all have both dorsal and ventral cirri. The dorsal are by far the more robust and reach their maximal length in segment 4–5. Branchiae are lacking and noto-trochs occur from segment 2 onwards. "Bacillary glands" are found in every segment after the second along the dorsal median line. The number varies from two to four or more per segment. They can be arranged segmentally in a circle or also irregularly scattered. The pygidium is tapered, pigmented brown, and has no cirri.

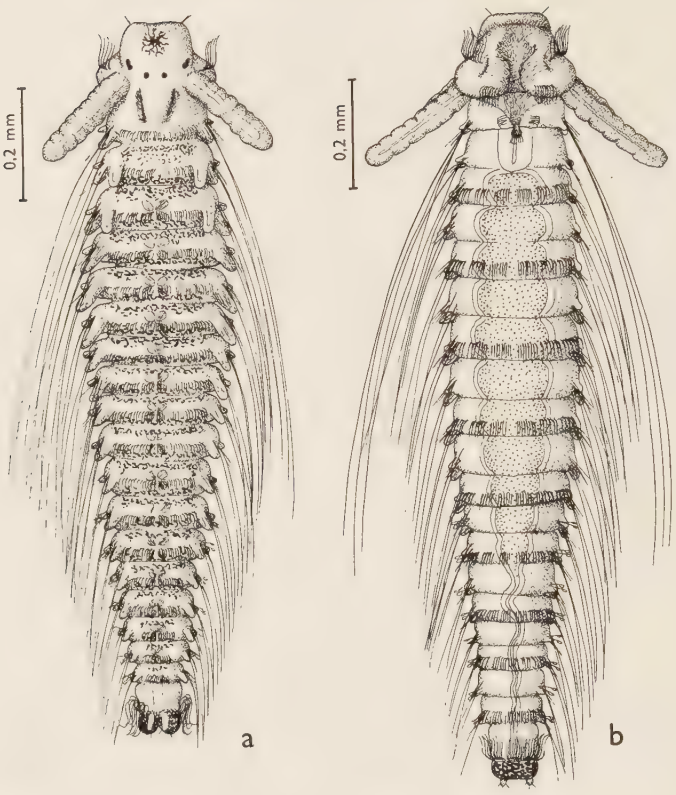


Fig. 22. *Spio theeli* (Söderström). a) and b) Pelagic larvae (dorsal and ventral view).

Dorsally on the prostomium there is a median melanophore. Otherwise the dorsal side has a diffuse brownish pigmentation. The larval setae are long, thin and rather lustreless. Of adult bristles there are both dorsal and ventral hairy bristles, but hooded crochets are lacking.

The larva ready to metamorphose (figs. 22a–b)

The description is based on the 19-segment stage.

The prostomium has become rounded and the "nuchal crest" has been further extended posteriorly. The palpi have attained a length of about 3 segments. In segments 2 and 3 branchial anlages have appeared. The pygidium has acquired a terminal notch and also a pair of dorsal anlages to cirri, which bear fine tactile cilia. The pharynx has become pigmented orange, and extends through segment 2. Near the anus the rectum is pigmented brown. The stomach has most often brownish-green contents. Of adult bristles there are both dorsal and ventral hairy bristles in all segments, and from segment 11 onwards also ventral hooded crochets. The

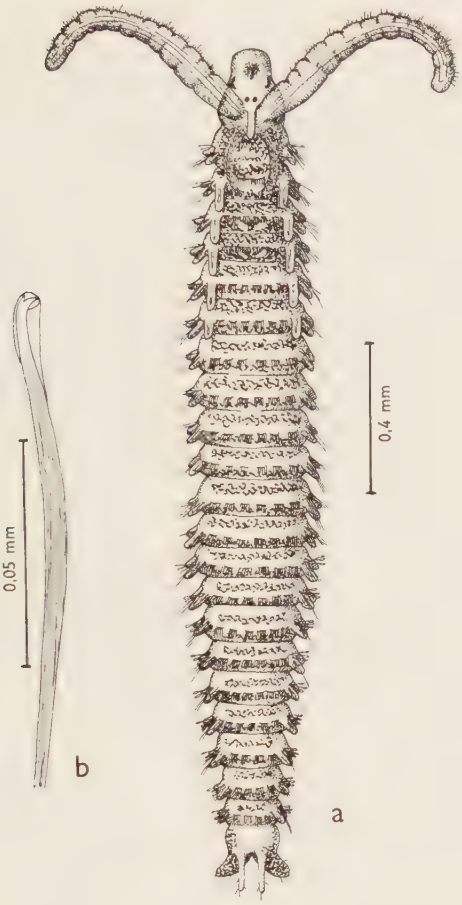


Fig. 23. *Spio theeli* (Söderström). a) Young bottom stage (dorsal view). b) Ventral hooded crochet from the same.

latter are long, coarse, and disserated. The lateral serration is short and stumpy. A "ciliated pit" is located in segment 2 and is surrounded by a pair of ciliated cells. The gastrotrochs consists of six cells each, and appear in every other segment from the third onwards.

The young benthonic stage (figs. 23a–b)

The description is based primarly on a specimen with 21 segments.

The prostomium has undergone considerable extension and has acquired a terminal rounding at the tip. The melanophore on the prostomium characteristic of the larva is still unaltered. The nuchal crest has grown posteriorly, and has become rather narrower. The palpi are robust, richly ciliated, and completely colourless. The nucal organs have attained the generically typical

horseshoe shape. The nototrochs in segment 2 are entirely enclosed by this structure. Paired dorsal organs occur in the anterior segments from the third. They are reniform and orientated with the concave side directed towards the median line. The parapodial cirri have increased in length. The dorsal ones are still longest in the middle section of the body. The ventral cirri are of about equal length in all segments. Branchiae are found in segment 2 and the five succeeding ones. In the pygidium also a pair of ventral cirri have been formed, and thus it has acquired the generically typical appearance. The dorsal pigmentation is concentrated at the segmental boundaries. Dorsal and ventral hairy bristles are found in all segments. They are "winged" and attain a length of 0.20 mm dorsally, and 0.16 mm ventrally. The ventral ones are more curved than the dorsal. Ventral hooded crochets are still observed from segment 11 onwards (fig. 23b). There are three in each neuropodium, and they are accompanied by three simple, thin, hairy bristles.

Identity of species

For several reasons (the structure of the nuchal organs, appearance of the pygidium, etc.) the species must be sought in the genera *Spio* or *Microspio*. The structure of the prostomium, formation of the parapodia, location of the branchiae, type of the dorsal organs like the appearance of the hooded crochets substantiate my classification of this larva as *Spio Theeli*.

Biology

The metamorphosis is induced by pure mineral sand. The worm builds stable tubes of a secretion and sand grains. It feeds readily on detritus, planktonic organisms, etc.

Literature

It is probable that the larva which Thorson (1946) described as "*Spionid larva C*" is identical with the one described here. This view is supported by the size, pigmentation, period of maximal abundance in plankton, etc. of this larva.

Spio martinensis Mesnil

Occurrence in the area of investigation

The species occur very numerously upon sand bottom at depths from about ½ m to a few meters. It has not been previously described from Sweden. It is, however, conceivable that this species is identical with *Microspio arctica* Söderström. Young individuals agree remarkably well with the description of this species. *Microspio arctica* is known from Ore Sound (G. Thulin according to Söderström 1920).

Larval types

Two larval types, both of which must be referred to this species, have been obtained in plankton. They diverge relatively markedly from each other in appearance. In the following I designate the two larvae as *Type I* and *Type II*. Of *Type I* 46 individuals were cultured during the period October 9, 1952 to January 7, 1953. At the examination, the benthic life had therefore lasted for about three months. The different individuals varied greatly in size and sexual maturity. The smallest had 20 segments, and the biggest 51. The average was 33.4 segments. About half contained sexual products of varying degrees of development. There were both males and females. Of *Type II* a similar number was cultured. Through a mishap unfortunately only 14 individuals were bread through a benthic life of sufficient duration. The experiment was begun on July 17, 1952, and the animals were examined on January 1, 1953. The benthonic stage had therefore then lasted about five and a half months. The size ranged between 35 and 48 segments. All contained sexual products of different degrees of development. There were both males and females.

The sexually mature individuals of these two larval types were found to be identical. The experiment shows that it cannot be a question of any sexual dimorphism, which becomes manifest already in the larval stage.

TYPE I

Occurrence in plankton

The larva occurs in plankton during the middle of the summer and in the autumn. It has been encountered on June 28 (1948) at the earliest, and rare specimens I have found as late as February 6 (1952). The maximum is appearently attained in September–October. At times the larva is very numerous, and for this reason has been a suitable object for investigations into metamorphism (p. 185).

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
7	0.58	0.16
12	0.80	0.18
16	1.16	0.24
19	1.62	0.26
24	2.19	0.32

Type I is in all stages smaller than *Type II* and never attains so great a number of segments before metamorphosis. Through its characteristic

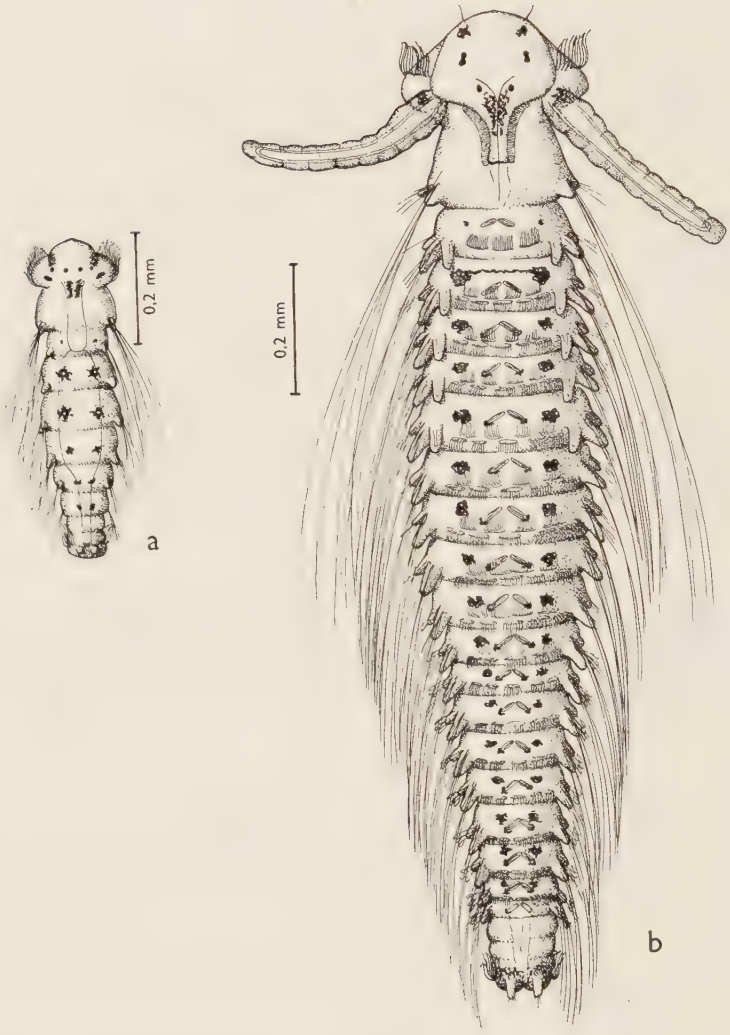


Fig. 24. *Spio martinensis* Mesnil *Type I*. Pelagic larvae. a) Young larvae (dorsal view). b) Larva ready to metamorphose (dorsal view). The head is somewhat deformed by pressure between the slide and the cover glass when figured. Normally the lateral lips are not spread out as in the figure.

dorsal pigmentation it can be readily distinguished from other species of the same genus.

The larva ready to metamorphose (fig. 24b)

The prostomium is rounded or has a slight notch at the tip. There are three pairs of black eyes. Palpi are formed in the 10-segment stage. In the

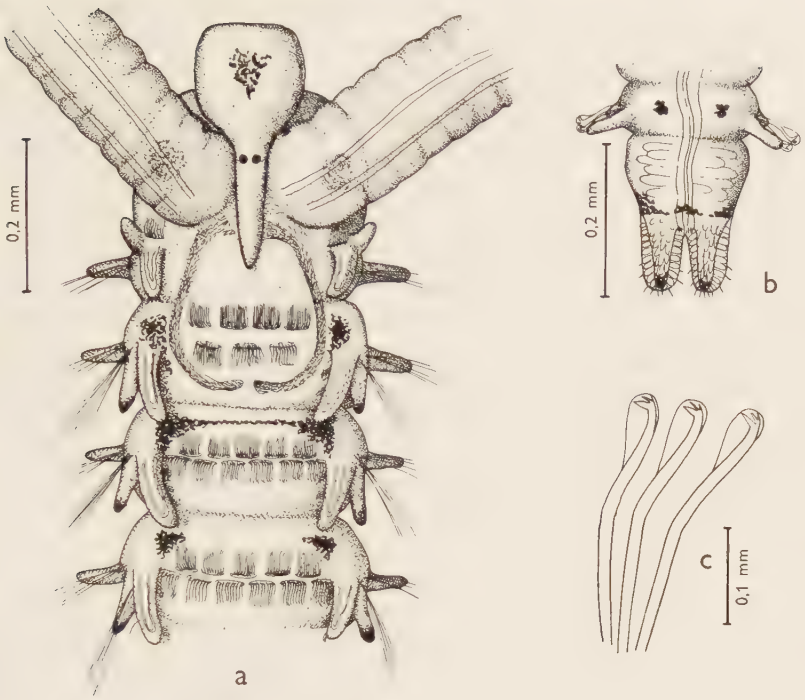


Fig. 25. *Spio martinensis* Mesnil *Type I.* Young bottom stage (22 segments). a) Fore part (dorsal view). b) Hind part (dorsal view). c) Ventral hooded crochets.

16-segment stage they have a length of about one segment. In older individuals they are often, but not always, provided with small, yellowish-white (reflected light) chromatophores. Anterior to the most median pair of eyes there is a pair of tactile cilia. The groove-shaped, longitudinal nuchal organs extend in the oldest larvae to the boundary between segments 1 and 2. Between them there is a low nuchal crest which terminates bluntly. Dorsal organs are lacking in the pelagic larvae. Parapodial, dorsal and ventral, cirri develop early. The dorsal ones are stronger except in segment 1 where the ventral ones are of about equal length. From the middle of the body onwards the dorsal cirri are black-tipped. In individuals with 16–17 segments branchiae begin to develop in segment 2. A larva with 18 segments has usually already five pairs of branchial anlages. The notochs are first uniserial and thereafter biserial. The posterior row is more robust and is composed of four ciliated cells. In older larvae dorsal and ventral cirri appear on the pygidium in the order named (cf. fig. 27b–d). Two rows of obliquely orientated "bacillary glands" are formed. They are pigmented black at their openings. The prostomium is pale brown. Ventrally on the peristomium a pair of yellow (reflected light) chromatophores is

found. The pharynx is strongly pigmented black. The dorsal side of segment 1 is completely colourless. In segment 2 and the succeeding segments there is a pair of melanophores. They are most strongly developed in segment 3. In the center of these melanophores there is often a little spot of white pigment (reflected light). Like the melanin it can be dispersed. Especially in older larvae it is frequently scattered in fine ramifications. When the pigment has once been dispersed it cannot collect again. The pygidium is pigmented brown and ventrally there often is a yellowish-white (reflected light) chromatophore. The pharynx extends in the oldest larvae to about segment 4. The stomach merges without any distinct boundary into the rectum. The larval setae are relatively long already in larvae with 7 segments, and thereafter grow rapidly. Of adult bristles both hairy bristles and crochets are formed already during the pelagic stage. Two to three ventral triserrated hooded crochets (fig. 25c) occur from segment 11 onwards in every neuropodium.

TYPE II

Occurrence in plankton

The larva occurs most abundantly in the beginning of July, when at certain times it can be predominant. It has been observed on May 29 (1948) at the earliest and latest on October 23 (1952).

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
15	1.42	0.25
21	1.80	0.33
27	3.12	0.46

The larva is characterized by its bigness and its characteristic pigmentation.

The larva ready to metamorphose (figs. 26a–b)

Here only a number of characteristics will be mentioned which distinguish this larval type from the foregoing.

In contradistinction to the foregoing larval type dorsal organs are developed in *Type II* already in the pelagic stage. They constitute hour-glass shaped, transversally located, colourless areas, which appear along the median line from the third segment onwards. They are situated in the posterior part of the segment, each half being equipped with two longitudinal rows of very thin and short cilia (fig. 27a). The nototrochs agree

with those in the foregoing larva except that they have a greater number of ciliated cells. The telotroch as well as the prototroch are relatively weaker. Obliquely orientated "bacillary glands" are lacking. The dorsal side has a fairly pronounced black pigmentation. Here, however, it is not concentrated in distinct melanophores but diffusely scattered. On the edges of the nuchal crest melanin forms a pair of narrow bands, which are characteristic of this larva (fig. 26a). In the anterior parts of the segments, and anterior and lateral to the dorsal organs there is an abundance of melanin, and in older larvae we find at times on the dorsal side also fine bands of a yellowish-white (reflected light) pigment which run transversally in the segments. In addition to the structured pigmentation there is a diffuse yellowish-brown pigment, which is especially prominent in the prostomium. The pharynx is pigmented brown and not black as in Type I. The oesophagus, which in older larvae extends roughly through segment 5, is completely colourless. The stomach, which opens into a slightly convoluted rectum, has a yellowish-brown or greenish-brown colour, and extends roughly through segment 15 in older larvae. Larval setae can both occur and be lacking. I have been unable to determine whether certain individuals are never provided with larval setae or whether these have been lost during capture. As in the foregoing larva the larval setae are relatively long, but are more strongly iridiscent in contrast. Dorsal adult hairy bristles occur both dorsally and ventrally in all segments. Ventral hooded crochets are found from segment 11 onwards, and are of the same type as in the foregoing larva. They are, however, still lacking in the 17-segment stage. The gastrotrochs are each composed of seven ciliated cells.

Metamorphosis can appearently be induced in the 24–25-segment stage in this larva compared with 17–18-segment stage in the foregoing.

TYPES I AND II

The young benthonic stage (fig. 25a–c, 27e, 28)

As previously mentioned these larval types develop identical bottom stages. About one month after the metamorphosis they can no longer be distinguished from each other.

The prostomium grows in length. One pair of eyes has been reduced. The yellowish-white (reflected light) cromatophores persist for a very long time, but are finally reduced. The parapodial cirri become prominent, but the dorsal ones in segment 1 remain insignificant for a long while. The dorsal cirri become leaf-shaped and tapered, the ventral likewise leaf-shaped but rounded. Branchiae are gradually formed even in the first setiger, and the number increases with increasing age until finally they occur in all but the last segments. The nuchal organs develop into the

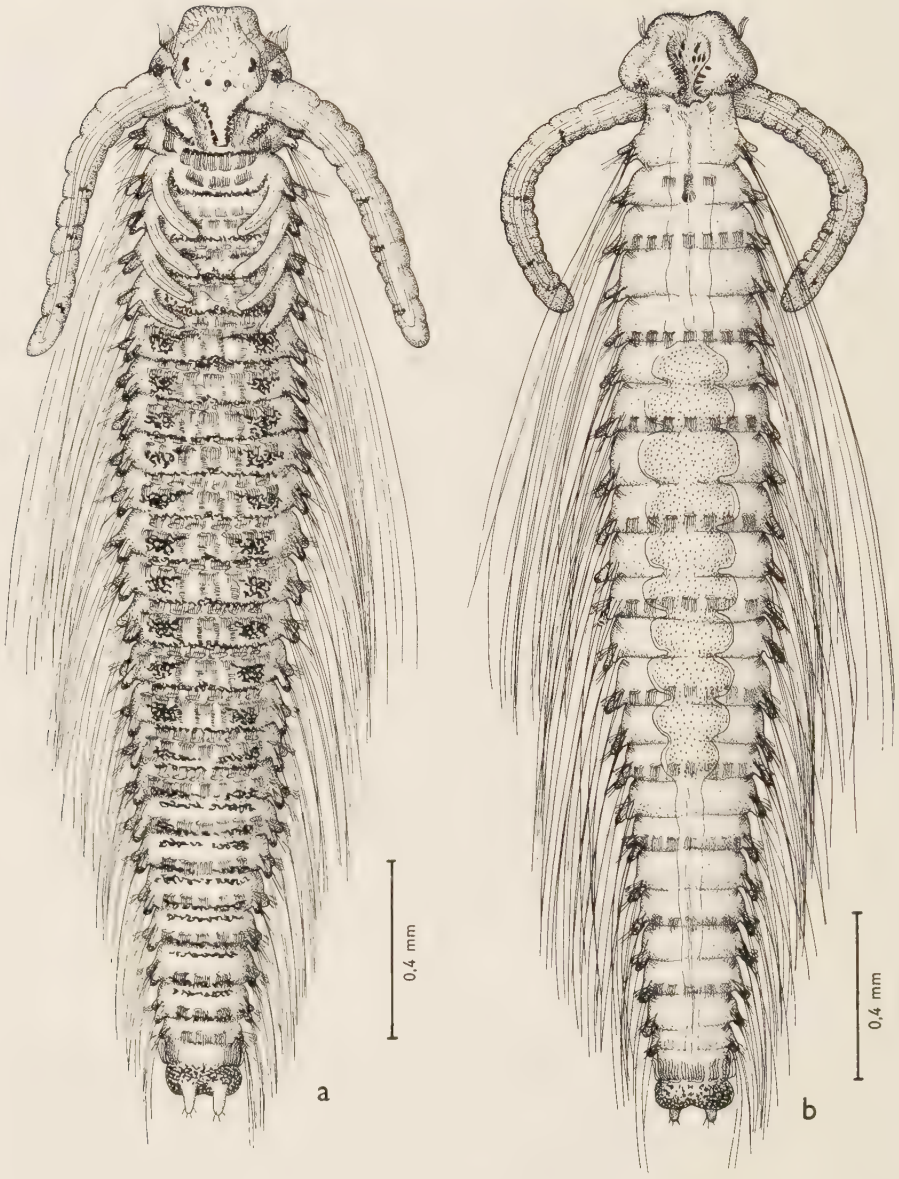


Fig. 26. *Spio martinensis* Mesnil *Type II*. Pelagic larvae ready to metamorphose. a) Dorsal view. b) Ventral view.

generically typical horse-shoe-shaped structure, and will include the nototroch in segment 2 (fig. 25a). In the larva of *Type I* dorsal organs are lacking as has been mentioned (p. 77). After the metamorphosis such structures are also formed here, and have exactly the same appearance and location as in the larva of *Type II*. Thereafter the dorsal organs divide

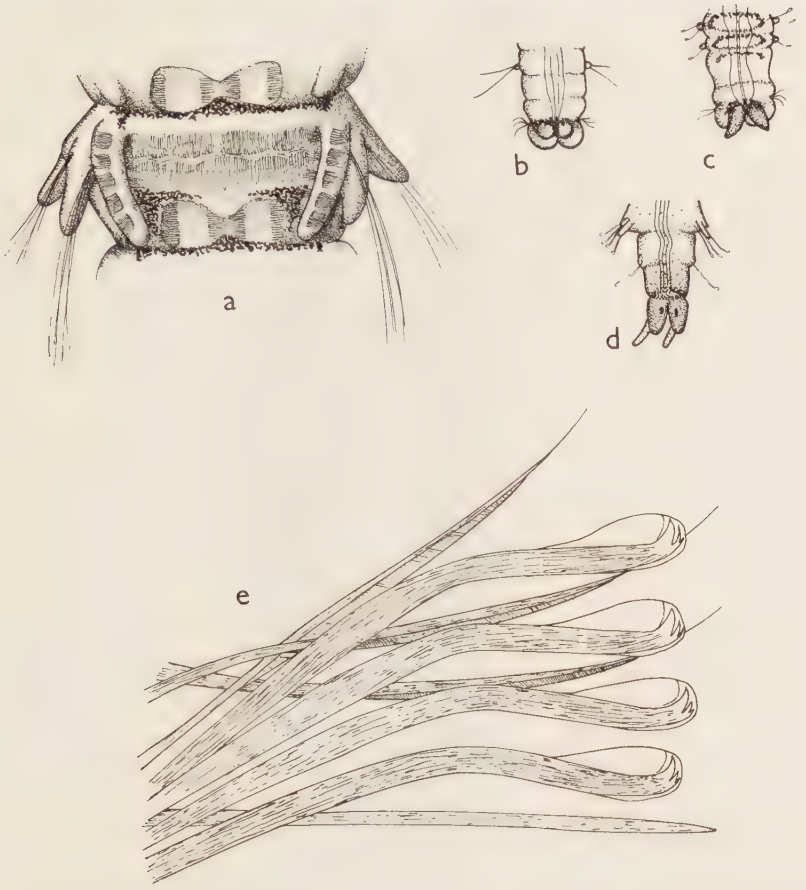


Fig. 27. *Spio martinensis* Mesnil *Type II*. a) Dorsal view of segment 5 of a pelagic larva with 27 segments. b)–d) The development of the pygidium: b) Pelagic larva with 20 segments. c) Pelagic larva with 27 segments. d) Young bottom stage (b and c dorsal views, d ventral view). e) Ventral bristles from a young bottom stage (34 segments).

in their median connection, and the halves migrate from the median line. Each half becomes distinctly demarcated from the surrounding epithelium as a shallow depression. The two longitudinal cilia bundles (see p. 78) develop into longitudinal ciliated areas separated by a non-ciliated region. In each segment, therefore, will occur four ciliated areas which are joined two by two in oval shallow depressions. In all bottom stages of sufficient age, regardless of the larval type from which they originate, the pigmentation is first scattered and most pronounced in segment 3. Most of the dorsal pigmentation is thereafter gradually reduced. The stomach becomes gradually pigmented brown, while the other parts of the digestive canal are unpigmented. The adult bristles increase in length but do not alter in

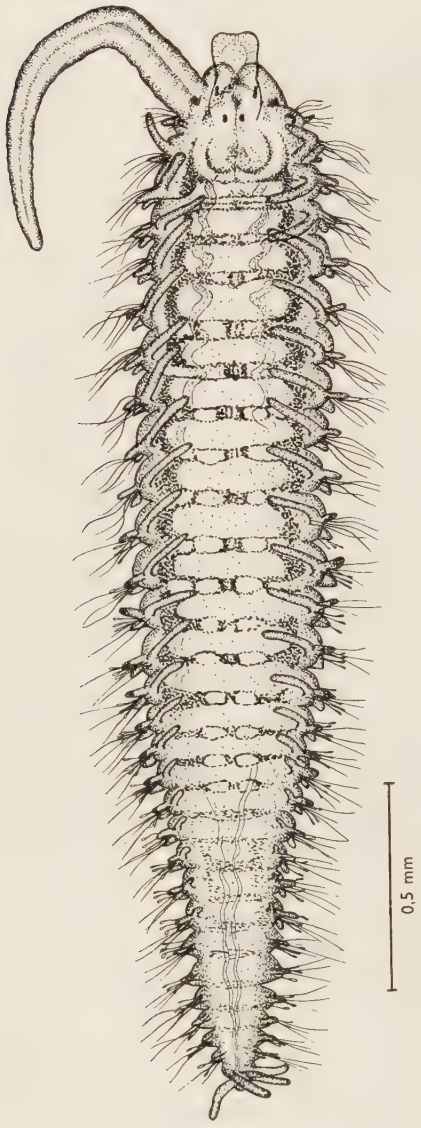


Fig. 28. *Spio Martinensis* Mesnil Young bottom stage (Dorsal view of a fixed specimen. Right tentacular palp lost.).

form, with the exception of the ventral hooded crochets which are diserrated in older individuals. It is the most distal serration which disappears in these, probably the result of wear and tear. For one can observe intermediate types, i.e. triserrated crochets with a very weak distal serration. The crochets are gradually eliminated in segments 11 and 12 and, therefore, in sexually mature individuals crochets begin first in segment 13 or

even farther posteriorly. The number of crochets usually amounts to four to six per neuropodium, and they are accompanied by a varying number of hairy bristles and one or two coarse, acicula-like, bristles (fig. 27e).

Identity of species

The recently metamorphosed worm agrees very well with the description that MESNIL (1896) has given of the species. Important characteristics are the occurrence of the branchiae, appearance and occurrence of the bristles, appearance of the dorsal cirri, etc. The identity of the species must be regarded as established.

Biology

Both larval types metamorphose readily in clean mineral sand, somewhat less readily in mud. They build tubes which protrude somewhat above the surface of the bottom substratum, and have branches below the surface. The worms feed on detritus, plankton, etc.

Literature

The species was described by MESNIL (1896). Later on (1897) he made a comparison between *Spio martinensis* and the rather closely connected *Spio filicornis* but found that it was a case of two distinct species. SÖDERSTRÖM (1920) combined the species with *Spio filicornis*. In a later work MESNIL (1925) maintained his view that *Spio martinensis* and *Spio filicornis* were two separate species. This is also my opinion. They differ from each other with regard to the occurrence of the ventral hooded crochets (from segment 10 onwards in *Spio filicornis* and from segment 13–15 in *Spio martinensis*), and also in the larval development. It is on the other hand disputable whether *S. martinensis* can be considered as a uniform species, as will be discussed in the following.

MESNIL in 1897 described the egg-capsules which are freely discharged in the bottom substratum. They are cylindrical, flattened, and contain several rows of eggs. CAULLERY and MESNIL (1917) found that there were actually two different types of egg-capsules which they named "Ponte A" and "Ponte B". The former type occurred most abundantly in April, had a length of 10–16 mm, and contained eggs of 150 μ in diameter, which had a yellow colour. "Ponte B", on the other hand, did not exceed 10 mm in length, contained eggs with a diameter of 130 μ, and occurred chiefly in the later part of the summer. The eggs in the first-mentioned capsule developed into larvae which were hatched at the 3-segment stage. In "Ponte B", on the other hand, not all the eggs did develop. Certain eggs disintegrated and served as food for the growing larvae. This condition was called adelphophagia by the authors. The larvae in "Ponte B" were not hatched

before the 15-segment stage and lacked the generically typical larval setae. Unfortunately these authors gave very brief descriptions of both egg-capsules and larvae, and no figures occur except for one of the types of egg-capsule. This has created some difficulties in identification. Mesnil and Caullery (1917) first thought that the species should develop different egg-capsules at different ages or, in other words, "Ponte B" should be formed at a first spawning and "Ponte A" at second. At the first the worms should therefore spawn in the later part ot the summer, and at the second in the earlier part of the summer of the following year. In a later work (Caullery and Mesnil 1918) they were inclined to regard the divergences in developmental type as seasonal dimorphism.

Mesnil (1896) described a larva which he classified as *Scolelepis girardi*. In 1897 he had, however, changed his mind and referred the larva to *Microspio atlantica*. Later (1925) he again revised his opinion and definitely stated that the larva should be classified as *Spio martinensis*, and that it was the one which develops from "Ponte A". He further pointed out at that time that the young individual has triserrated bristles, but that these become diserrated later. There is absolutely no doubt that the larva which I have described as *Type I* is identical with this one of Mesnil (1896, 1897, 1925). His figures and descriptions agree very well with my *Type I*. More recently this larval type has been described by other authors, who were, however, unable to identify its species. Hofker (1920) mentioned a larva, which he characterized as follows: "De metatrochophora is gekenmerkt door pigment an heit eind der dorsale cirren, door 2 onvertakte pigmentvlekken op den rug in elk segment, en door pigment rondom oesophagus." He referred this larva to *Nerine cirratulus*, but there is hardly any question that it is identical with *Spio martinensis Type I*. Thorson's (1946) "*Spionid larva F*" should also undoubtedly be considered identical with this one as well as Smidt's (1951) "*Pygospio elegans Type II*" (see p. 99). The larva which Thorson (1946) has described as "*Spionid larva E*" is presumably identical with the larva which I have described as *Type II*.

It is readily conceivable that the larva which I have described as *Type II* may be identical with the larva which Mesnil and Caullery (op. cit.) found to develop from the eggs in "Ponte B". I have never found larvae of this type with less than 15 segments. It is also at the 15-segment stage that the larvae of "Ponte B" should be hatched. Furthermore, I have found that certain larvae of this type may lack larval setae, Mesnil and Caullery reported, it is true, that larvae from "Ponte B" were developed without a pelagic stage. This, however, does not necessarily constitute a direct obstacle to the development of *Type II* from "Ponte B". It is, namely, known that *Pygospio elegans* exhibits all transitions between hatching to a pelagic life with a young stage provided with larval setae,

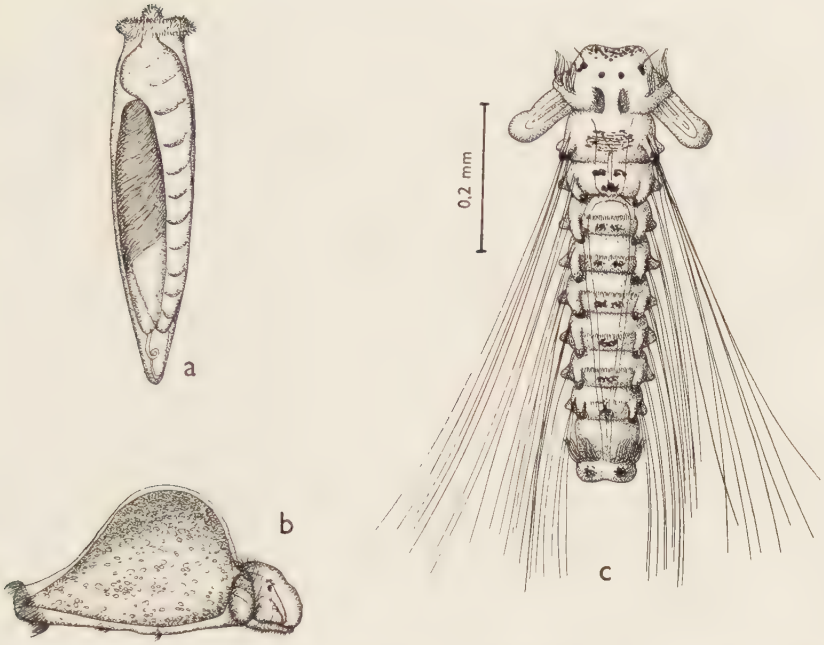


Fig. 29. *Microspio mecznikowianus* (Claparède). a) Spermiophor. b) Young larva from an egg capsule (a and b after Claparède and Mecznikow 1869). *Microspio atlantica* (Langerhans). c) Young pelagic larva (dorsal view).

and a direct development without a pelagic stage where such bristles are totally lacking.

The question may be left open for the time being as to whether it is a case of two closely related species, which strikes me as probable, or whether one and the same species is concerned, which during different periods of its life develops larvae of different types. It is, however, entirely clear that it is not a case of seasonal dimorphism in one species. Both larval types occur in plankton during the later part of the summer. In order to arrive at definite conclusions regarding these questions it is necessary to rear a number of specimens of both larval types through the entire life cycle —unfortunately a very difficult task.

Microspio atlantica (Langerhans)

Occurrence in the area of investigation

The adult worm has been encountered on a number of occasions in pure mineral sand at a depth of about 1 m in the bay of Kristineberg.

Occurrence in plankton

The larva appears as a typical midsummer form in plankton. It has been observed on June 22 (1947) at the earliest and latest on November 13 (1952). It seldom occurs in great numbers.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
8	0.66	0.12
10	0.80	0.20
12	0.90	0.20

The larva is appreciably smaller than those belonging to *Spio*. It is ready to metamorphose at the 12-segment stage. It is otherwise characterized by the three distinct melanophores situated in a triangle in segment 2.

The larva ready to metamorphose (figs. 30a–d)

A larva with 12 segments is described as typical of the stage.

The prostomium is richly set with tactile cilia, broad, and slightly notched terminally. There are three pairs of black eyes. In the dorsal aspect the lateral pairs coincide. The palpi are fairly long and robust, and are always borne in a characteristic manner extending from the body. They are distally pigmented yellow brown. At the proximal ends of the palpi are found small toric structures, each bearing a little bundle of cilia. The parapodia are differentiated early, and well demarcated from the body. This larva differs in this respect from those belonging to *Spio*. Welldeveloped dorsal and ventral cirri are found in all segments. The dorsal are longer and black-tipped. Branchial anlages are lacking. Complete nototrochs occur first from segment 3 onwards. In the two first segments they are represented by lateral bundles only. A marked intersegmental ciliation is observed. "Grasping cilia" are lacking. Pygidial cirri are not formed. The pygidium has a diffuse yellowish-green pigmentation. Dorsally is found a pair of black, and ventrally a pair of yellowish-white (reflected light spots). The telotroch is weakly developed. The prostomium has a yellowish-green colour. The dorsal pigmentation has a very characteristic pattern of melanophores. In segment 1 melanin forms narrow, dense, transversal bands. In segment 2 it is concentrated into three distinct, square, triangularly placed melanophores. In the following segments there is an anterior diffuse band of melanin and, behind, two distinct, square melanophores. In the most posterior part of the body these coalesce into one melanophore. A

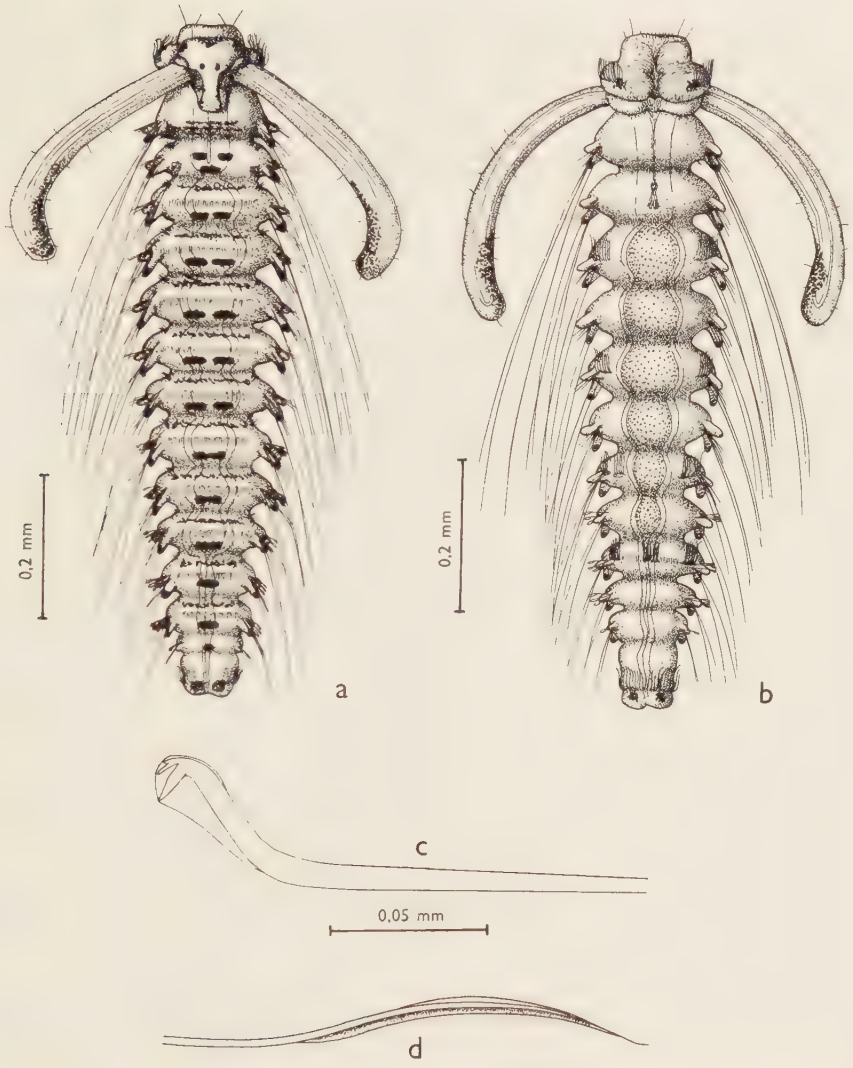


Fig. 30. *Microspio atlantica* (Langerhans). a) Pelagic larva ready to metamorphose (dorsal view). b) Pelagic larva ready to metamorphose (ventral view). c) Ventral hooded crochet from a pelagic larva. d) "Winged" bristle from the same.

muscular oesophagus extends through segment 2, where it merges into a thick-walled stomach. This is followed in segment 9 by a convoluted rectum. The larval setae are relatively thin and short. Of adult bristles there are both dorsal and ventral hairy bristles, and from segment 9 onwards also ventral triserrated hooded crochets. The under side of the peristomium appears, on account of a fold, to be divided into two successive sections (fig. 30b). Ventral to the proximal parts of the palpi there is a pair of

yellowish-white (reflected light) chromatophores. A "ciliated pit" is located in segment 2. The gastrotrochs are of a divergent type. They occur in segments 3, 5, 7, and 9. In segments 3 and 5 they are represented by a pair of lateral ciliated cells only. In segment 7 there are two ciliated cells on either side, and in segment 9, finally, there are one median and two lateral cells joined by a shorter ciliation.

The young benthonic stage (fig. 31)

The description is based mainly upon one individual, examined two months after metamorphosis, which had 35 segments and a length of 8.5 mm, and three individuals of the same age, which were somewhat smaller.

The prostomium is extended and somewhat notched at the tip. It is slightly pigmented brown. There are only two pairs of eyes. The median ones are rounded, and the lateral reniform double-eyes. The palpi are very long, somewhat longer than the entire animal, and very fragile. They are provided with three to nine rings of a yellowish-white pigment (reflected light), and somewhat broader proximally than terminally. The nuchal organs are of the same type as in adult specimens of *Spio*. They extend posteriorly through segment 2. In their most posterior parts they diverge from each other with a very slight curve. These most posterior parts resemble the dorsal organs occurring in the next segment. In all segments the parapodia have both dorsal and ventral cirri. In segment 1 they are smaller than in the succeeding. In segment 1 the dorsal cirri are provided with a little terminal notch, and closely pressed into the bases of the palpi. On their most median part they bear a little bundle of cilia. In the following segments the dorsal cirri are considerably more robust than the ventral ones. At first branchiae are formed in segment 3. Later branchiae appear also in segment 2 and in the succeeding segments. A nototroch occurs in all segments from the second onwards, where it is composed of six ciliated cells arranged in two rows, which are enclosed by the nuchal organs. In the succeeding segments they consist of two rows of ciliated cells with six cells in each. There is a well-developed intersegmental ciliation. The pygidium is of the same type as in *Spio*. Remains of larval melanin pigmentation still persists after two months. The unpigmented oesophagus extends through segment 7. The stomach, which is pigmented brown, extends through segment 12, where it is followed by a convoluted rectum. Hairy bristles are found in all segments. In segment 1 there are only ventral ones. The dorsal hairy bristles are appreciably longer than the ventral ones. From segment 9 onwards there are ventral triserrated hooded crochets (fig. 30c). Of these there are two or three in each neuropodium, and they are accompanied by four or five hairy bristles.

Both males and females were found among the cultured specimens.

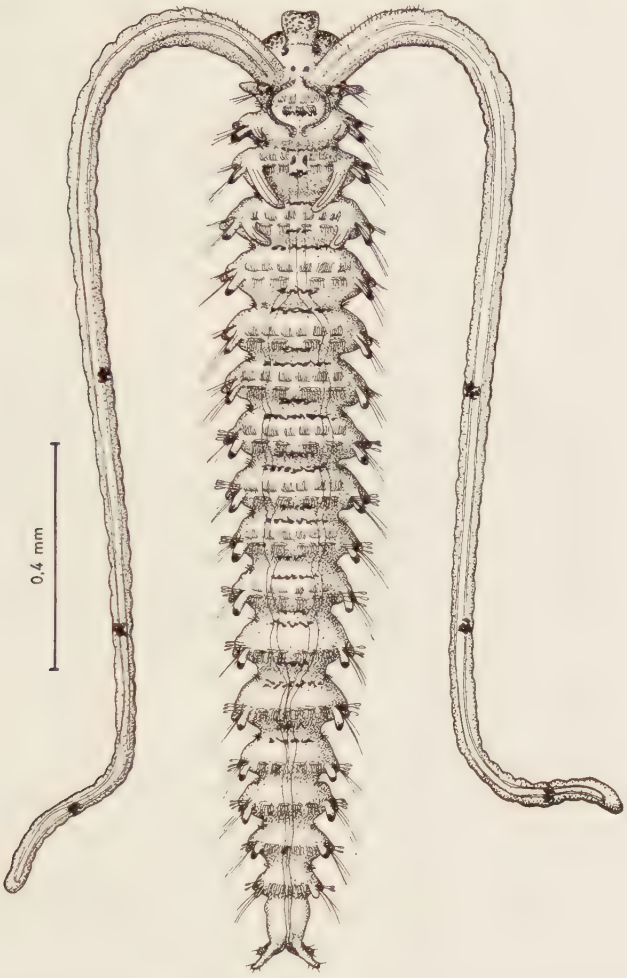


Fig. 31. *Microspio atlantica* (Langerhans). Young bottom stage (dorsal view).

Sexual products were observed from segment 15 onwards. One male, which had been reared for two months, had very large epitoquous nephridia of the type described for *Microspio mecznikowianus* (Cerruti 1908) and which occur in considerably weaker development in, for example, *Spio martinensis*.

Identity of species

The appearance of the nuchal and dorsal organs, and of the pygidium is such that the species can be referred to *Spio* or *Microspio*, without further discussion. The lack of branchiae in segment 1, and the occurrence of typical

triserrated bristles ventrally from segment 8–9 onwards speak in favour of *Microspio atlantica*.

Biology

The largest of the bottom stages examined had after two months built an approximately 7 cm long tube of sand and a secretion. This tube was branched and lay close to the surface of the substratum. The species appears to feed on detritus.

Literature

Langerhans (1881) first described this species under the name of *Spio atlanticus*. Mesnil (1896) formed the genus *Microspio* for *Spio atlanticus* Langerhans and *Spio mecznikowianus* Claparède. He pointed out that the first-mentioned species had ventral crochets from segment 9 and the latter from segment 11 onwards. Söderström (1920) combined the two species under *Microspio mecznikowianus* (Claparède). Since the larva described here have ventral crochets from segment 9 onwards after having reached sexual maturity (a number of adult specimens from the area of investigation also had this characteristic) I consider that the re-establishment of *M. atlantica* as a independent species is justified.

Up to now the development has been entirely unknown. The spermatophores and early development in the closely related *M. mecznikowianus* have, on the other hand, been treated by a few investigators. Kölliker (1848) discovered peculiar structures in the sexually mature animal, which he regarded as gregarinae. That he had misunderstood the nature of the structures was demonstrated by Claparède and Mecznikow (1869), who found that they were formed in the epitoquous nephridia of the male and must be regarded as spermatophores (fig. 29a). Also the manner of construction was described in detail in this work. Claparède and Mecznikow (op. cit.), furthermore, described for the first time the type of egg-capsules, which later have been recovered from so many species belonging to *Spionidae*, and also young larvae from such capsules (fig. 29b). Cerruti (1908) re-examined the spermatophores and studied their manner of formation.

Pygospio Claparède

The egg and sperm

The egg has a thin egg-membrane, lacks membrane vesicles, and is exceedingly rich in yolk. The sperm has a long head and a demarcated movable acrosome. Spermatophores are formed in the epitoquous nephridia.

Type of development

Fertilization is preceded by a copulation. The development takes place to a greater or lesser degree in cuticle-like egg-capsules, fastened in the female's tube. Here the larvae subsist on unfertilized eggs, weaker embryos, and disintegrated eggs, i.e. adelphophagia. The duration of brood protection is dependent upon season. During the phase of pelagic development the larva is predominantly planktotrophic.

The pelagic larva

The larva is small and thick in relation to its length. The prostomium is stumpy, and the peristomium is poorly demarcated from the prostomium. Palpi are formed. There are three pairs of black eyes of which the most lateral are double-eyes. Nuchal organs are formed. Branchial anlages are lacking in all pelagic stages. Nototrochs occur from segment 2 onwards. The pygidium is rounded and lacks appendages. The telotroch is well developed and dorsally discontinuous. Only black structured pigment occurs. The larval setae are short, thin and lusterless. A "ciliated pit" is lacking. Gastrotrochs occur in segments 5 and 7.

1. Only one species, characterized by the foregoing. *Pygospio elegans.*

Pygospio elegans Claparède

Occurrence in the area of investigation

This species is particularly common on sand bottom to about 2 m deep.

Sexual maturity and hatching periods

On February 12, 1952, a great number of larvae belonging to this species were obtained in plankton. The number of segments varied from six to twelve. Two weeks later a number of egg-capsules were examined which had been freed from tubes belonging to this species. I found that the majority contained about 70 eggs or embryos. In addition there was a yolk mass, which must have come from disintegrated eggs. Unfortunately I did not succeed in getting larvae from these capsules to hatch. Findings of the pelagic larvae indicate that hatching can occur at the 6-segment stage or earlier. In July 1951 a large number of egg-capsules had been examined. Here larvae with up to 14 segments had been found, three to seven per capsule. Females with tubes containing egg-capsules (this can easily be ascertained by careful scraping off the sand grains from the hyaline inner wall of the tube, when the egg-capsules will become visible) had been transfered into cultures. On several occasions hatching took place in these. The hatched larvae had between 12 and 14 segments. These larvae were of

exactly the same type as those which I later found in February (corresponding stages). There are, therefore, no morphologically divergent larval types in different seasons (see p. 98). On the other hand, the brood protection varies in duration according to season. In winter the hatching occurs at least at the 6-segment stage (at least in many cases). During the summer it is impossible to find so small *Pygospio* larvae in plankton. The hatching takes place at that time at a considerably more developed stage. The pelagic stage is then very short. This explains why *Pygospio* larvae on the whole are very rare in summer plankton. I have found that the pelagic phase in July lasted only a few or 24 hours at the most, if substratum from the natural biotope was available.

Presumably all transitional forms between the reproductive types outlined in the foregoing exist. *Pygospio* larvae are continually encountered in plankton from February to August (during summer they are, however, rare).

Size of the larva

Segments	Length mm	Width mm
3 (from egg-capsule)	0.33	—
7.	0.42	0.15
12.	0.65	0.20

The 3-segment stage (fig. 32a)

On July 7, 1951, a number of larvae in the 3-segment stage were freed from an egg-capsule. Since these larva, which are markedly distended by yolk, are already well known (Söderström 1920, etc.) they will not be treated in detail here. It was shown that these freed larvae were able to survive in spite of the fact that they could not leave the bottom of the bowl by swimming, due to their abundance in yolk.

The 8-segment stage (fig. 32b)

Four days later these larvae had acquired five more segments and were now capable of swimming freely in the bowl, after the large yolk mass had been largely resorbed. The prostomium in this stage is rounded and provided with "bacillary glands" and numerous tactile cilia. The larval setae have increased in growth in segments 1–3. In segment 4 new ones have appeared. The alimentary canal is differentiated into three divisions. The oesophagus extends through segment 2, followed by the stomach which extends to the boundary between segments 4 and 5. The rectum is straight. In the posterior segments faint, dorsal, melanin bands are discernible.

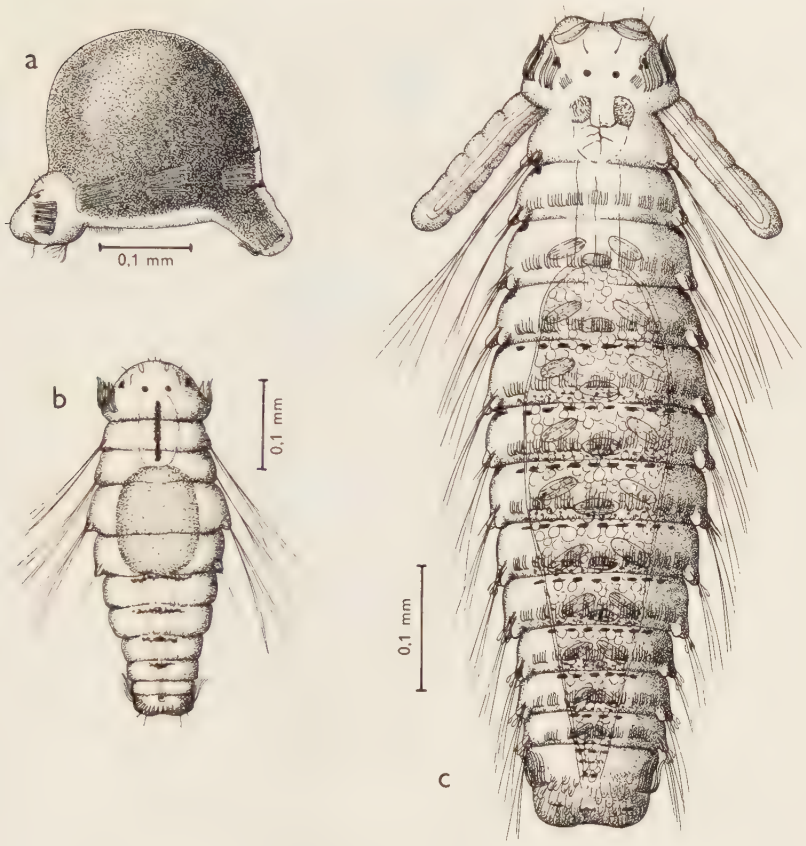


Fig. 32. *Pygospio elegans* Claparède. a) 3-segment-larva from an egg capsule (lateral view). b) Young pelagic larva (dorsal view). c) Larva ready to metamorphose (dorsal view).

Otherwise it is unpigmented. The pygidium is rounded and has several "bacillary glands". The telotroch is well developed. The parapodia are weakly differentiated, and nototrochs are lacking.

The larva ready to metamorphose (figs. 32c, 33)

On July 21, thus 14 days after the larvae had been freed in the 3-segment stage, they had acquired 12 segments. The prostomium has now been widened, and the tip has acquired a slight notch. There are still three pairs of black eyes. The lateral ones on each side coincide when seen from above. Several tactile cilia have appeared. In the posterior part of the prostomium there is a pair of nuchal organs. Palpi have developed. They have a length of about three segments. In the parapodia are found both dorsal and ventral cirri. Branchial anlages are lacking. Nototrochs occur from segment 2 onwards. The pygidium has not yet acquired any cirri. The number of

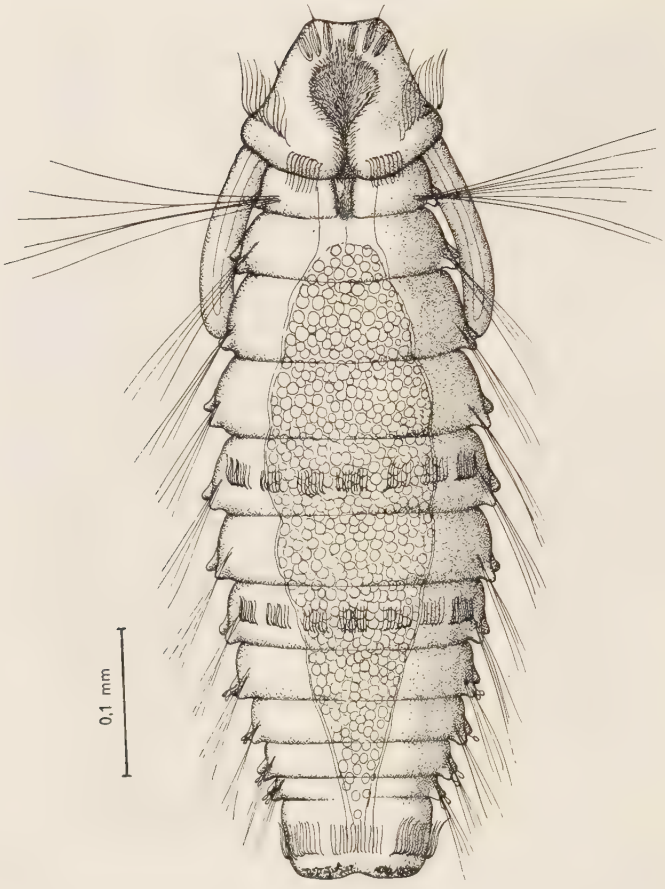


Fig. 33. *Pygospio elegans* Claparède. Old pelagic larva (ventral view).

"bacillary glands" has increased. Three to four occur dorsally in each segment, and can be very regularly arranged. A distinct, dorsal pigmentation has been formed. Laterally in the anterior part of segments 2–6 there is a large melanophore. From segment 3 4 and posterior thereto there is found in each segment a transverse band of small distinct melanophores. The pigmented area narrows into a tip towards the pygidium. On the latter is found also a transverse band of small melanophores. A colourless or somewhat darkly pigmented pharynx extends through segment 1, where it merges into a likewise weakly pigmented oesophagus, which extends to segment 3. The stomach, which generally has brownish-green contents, opens into the anus without any intervening rectum. Of adult bristles there are "winged" hairy bristles (fig. 34b) and ventral hooded crochets (fig. 34c). The latter occur from segment 8 onwards. The larval setae are relatively short and lustreless. The prototroch extends quite for down

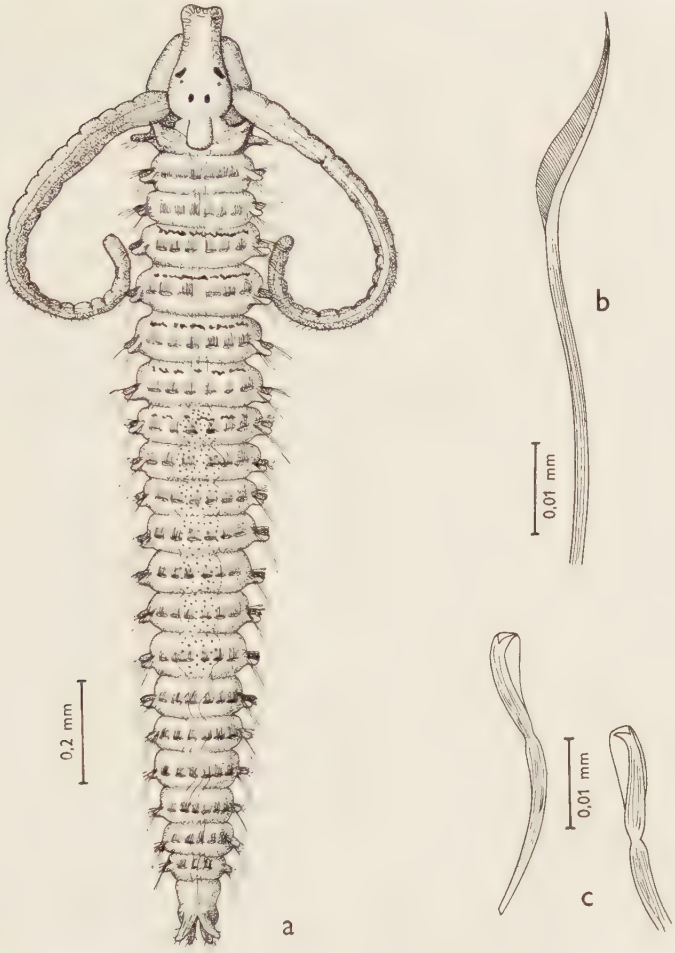


Fig. 34. *Pygospio elegans* Claparède. a) Young bottom stage (dorsal view). b) "Winged" bristle from fore segment of a pelagic larva. c) Ventral hooded crochets of the same.

ventrally. A neurotroch is found in segment 1, but there is no "ciliated pit". Perhaps a ventral median depression in segment 1 may be interpreted as a remainder of a reduced "ciliated pit". Gastrotrochs occur in segments 5 and 7.

The young benthonic stage (figs. 34a–c)

The description is based chiefly on some individuals with 19–21 segments.

The prostomium has undergone a considerable extension and is somewhat notched at the tip. There are still three pairs of eyes. The nuchal organs have developed into a pair of transversally placed, ciliated areas on either side of a low nuchal crest. The parapodia are provided with well

developed dorsal and ventral cirri. In segment 1 the cirri are large and anteriorly directed. (None of the young specimens which I have examined have had dorsal appendages in segment 2, belonging to the dorsal organs. These were lacking even in three months old specimens.) The branchiae are not yet developed. The pygidium has acquired the four, generically typical, cirri. The pharynx extends through segment 1. (In some individuals the pharynx has a slight dark pigmentation.) The unpigmented oesophagus has undergone a considerable extension and reaches beyond segment 7, were it merges into the somewhat brown-pigmented stomach. The rectum is convoluted and begins in segment 14. The adult hairy bristles, which occur dorsally and ventrally in all segments, are strong and provided with a "wing". Ventral hooded crochets (four per parapodium) are found in segment 8 and the succeeding segments.

Biology

The larva in all stages is strongly photopositive, an attribute which naturally is of the greatest significance for an eulittoral form like this. The metamorphosis is induced by mineral sand from the natural biotope after the larva has attained the 12–14-segment stage. The worm builds a very firm tube of a secretion and sand particles and is most often brown-coloured. The worm stays in the mouth of the tube, where it catches detritus and planktonic organisms by means of the palpi. The mouth of the tube is provided with a closing arrangement, which becomes visible when the worm withdraws. It consists of three triangular flaps, which are attached to the mouth of the tube at their bases. The two other sides of each triangle are free. When the worm retracts the triangles spring together, forming a three-sided, outwardly directed pyramid. It is conceivable that this closing mechanism is a protection against smaller predacious animals, which live in the sand. There are a number of small sand polychaetes, among others, young *Nephthys hombergi*, which are eating Spionids.

Further development of the benthonic stage in the natural biotope

Thirty individuals from a depth of 0–1 m in the bay of Kristineberg were examined on November 16, 1952. Four of these were considerably larger than the others. The number of segments cannot be stated as all specimens were mutilated. They had sexual products in the coelom in contrast to the others. In all probability these individuals represented the older generation, i.e., the one which had mostly spawned in the period February–August. It looks as if a small percentage of the population never propagates for some reason or other. Three of these larger individuals were females and one was a male with very large appendages in segment 2. The other specimens were considerably smaller, had no more than an aver-

age of 35 segments, and lacked sexual products. The dorsal appendages in segment 2 were not found in any of them. Another group was examined on December 14, 1951. Of about 40 individuals none had either sexual products or dorsal appendages in segment 2. A very appreciable growth had, however, taken place, and the average number of segments was 45. Thus no spawning occurs here during the winter months. During January and February 1952 the locality was uncovered at times on account of low water, and the bottom was frozen. Nevertheless, the place abounded with animal life when visited on February 29. Four Spionid species were found, among them even *Pygospio elegans*. The growth had, however, been very poor. In 13 examinated specimens the average number of segments was only 46. A large number of individuals, unfortunately mutilated by manipulation, were collected on the same day and examined with regard to the degree of maturity of sexual products. I found that 12 of 29 had mature sperms or eggs in the coelom. Others totally lacked such. The males had now dorsal appendages in segment 2. Some days later, individuals with egg-capsules containing embryos were also found in this locality.

Literature

The literature concerning the larval development of *Pygospio elegans* is rather extensive. Leschke (1903, p. 122, pl. VI, figs. 7–9) is probably the first who described the pelagic larva, which he found at Kiel. Thereafter it was treated by Gravely (1909, pl. III, fig. 38). He classified the larva, which he called "*Spio*" only provisionally under this species. The description and pictures are so incomplete that an identification must needs be uncertain. Söderström (1920) made the discovery that *Pygospio seticornis* Mesnil and *Pygospio elegans* Claparede only represented males and females of one and the same species. The earlier division had been based on a sexual dimorphism. Furthermore, Söderström described for the first time the egg-capsules and spermatophores. Egg-capsules were only known at that time in *Polydora*, *Microspio*, and *Spio*. In the egg-capsules there were larvae in different developmental stages, and he gave a good description of the young 3-segment larva, which is strongly distended by a mass of yolk (see p. 92). On comparing the number of eggs in a capsule with the number of larvae, which developed from them (40 50 compared to 6 7) he was able to conclude that the majority of eggs and the embryos had to serve as food for a few which developed further. This condition was then known in *Spio martinensis* (Mesnil and Caullery 1917, see p. 83). Söderström, who made his observations during the summer, found a capsule with larvae which had 16 segments. From this he drew the conclusion that the species propagated during the summer without any pelagic stage. In Kieler Föhrde, however, Leschke (op. cit.) had during March

found larvae in plankton which must belong to this species. SÖDERSTRÖM now concluded that *Pygospio* had two types of development, i.e., a pelagic one in the spring, and one without a pelagic phase in the summer. He drew certain parallels with the development in *Spio martinensis* described by MESNIL and CAULLERY (op. cit.). In my investigations I have been able to demonstrate that his teories were on the whole right.

THORSON (1946) supported SÖDERSTRÖM's conception. He studied egg-capsules from this species and found in them three to five larvae of the type described by SÖDERSTRÖM. The largest larvae, which he ever found in an egg-capsule, had eight to ten segments. At the same time THORSON described three different pelagic larvae types, all of which he referred to this species, viz.:

A. "*Small dark larvae with long larval bristles*". This larva is unfortunately described without pictures. It did not acquire more than eight to nine segments before undergoing metamorphosis. The gut was green, but it often had a bluish-black pigment and was thick-walled. Furthermore, the larva had three pairs of eyes and very long larval setae. It occurred throughout the year, but had its maximum during the latter part of the winter and spring. It is difficult to identify larvae after such a brief description without help of illustrations. I have, however, not found any *Pygospio* larva which metamorphoses at such an early stage as the one stated.

B. "*Large colourless larvae with short larval bristles*". These larvae were appreciably larger than the preceeding and attaind a length of 1.6–2.3 mm. They had three pairs of black eyes, a stomach with green contents and a pharynx with reddish-brown pigment. The pygidium had a yellowish-brown pigmentation on the dorsal side and a greenish pigmentation on the ventral with spots of black pigment. Near the anus the intestine was provided with black pigment. All segments were provided with small grains of bluish-black pigment on the dorsal side. This description agrees well with the larva which I have placed under *Spio multioculata*. It is really only the length of the larval setae which differs. Since these provisional bristles are easily discarded, this is not necessarily of any significance. The identity is supported by the fact that THORSON's larva is encountered in plankton during the same season as the larva of *Spio multioculata*. On the other hand, I have not discovered any *Pygospio* larva with which it could be identical.

C. "*Transitional stages between the small and the large larval types.*" This larva agrees with the long well-known *Pygospio* larva (LESCHKE op. cit., SÖDERSTRÖM op. cit.).

THORSON believed that there was still another type of development, which completely lacked the pelagic stage. This larval polymorphism, according to THORSON, should have appeared as a consequence of different degrees of brood protection. One kind of capsule should produce one larval

type, and another kind with a different nutrient supply should give rise to a second larval type, etc. He was, furthermore, of the opinion that there should be transitional types.

Finally SMIDT (1951, pp. 54–63, figs. 22, 23, 24) treated the reproductive biology of the species. He could not prove any development through adelphophagia. All the eggs developed into pelagic larvae. This is even more remarkable, inasmuch as SMIDT carried out his observations during the summer and early autumn. In spite of the fact that SMIDT did not find any differentiation in the developmental types with regard to the nutrient supply, he described three different pelagic larvae, all of which he found to metamorphose into *Pygospio elegans*. He obtained only one of them from egg-capsules, viz. "*Type I*". His larval types were the following:

"*Type I*". This larva agrees both by description and by illustration with the long and well known *Pygospio* larva (see the foregoing). An exception, however, must be made for the recently metamorphosed worm, which is figured with lateral prostomial processes. I have not found such processes in any of the young benthonic stages of *Pygospio*, which I have examinated. They are, however, characteristic of *Spiophanes bombyx* (see p. 35).

"*Type II*". This larva is larger than the foregoing. It differs from it by having dorsally two rows of black pigment spots and black pigment in the pharynx. This larva strongly resembles the one I have described as *Spio martinensis Type I* (p. 75). I base this contention mainly on the similarity in dorsal pigmentation with paired melanophores in each segment, of which the largest occur in segment 3, the size, and the dark pigment in the pharynx.

"*Type III*". This larva differs from the two preceding ones in its diffuse, dorsal pigmentation, the occurrence of reddish-brown and yellow pigment on prostomium and pygidium, black pigment at the anus, and lateral prostomial processes in older larvae (fig. 24b). In my opinion all these characteristics clearly indicate that the larva must belong to *Spiophanes bombyx*. SMIDT considered that "*Type III*" should be identical with THORSON's (loc. cit.) "*B. Large colourless larva with short larval bristles*", which I have shown (p. 71) should probably be identical with my *Spio multioculata* larva.

Otherwise a critical comparison of THORSON's and SMIDT's *Pygospio elegans* larvae reveals that only two of them are comparable, viz. THORSON's "*C*" and SMIDT's "*Type I*". These larvae in turn agree very well with those which have already been described as *Pygospio elegans* (LESCHKE op. cit., SÖDERSTRÖM op. cit.). In fact it is the only larva which I have found to belong to this species.

Summary

1. *Pygospio elegans* propagates during the period February-August.
2. The development always takes place to a certain extent in egg-capsules.

3. In the capsule the young larva consumes eggs and young embryos, which are less developed.

4. The time during which the larva remains in the capsule varies. During the spring it is short, and during the summer long. In spring the larvae have a long pelagic stage, and in the summer a short one. It is probable that the pelagic phase in certain cases (during the summer) can be completely eliminated.

5. During the entire reproductive period larvae are produced of only one morphologic type, regardless of whether the brood protection is prolonged or brief.

6. The species is annual and dies after spawning.

7. The development of the benthonic stage proceeds rapidly during the autumn months, and very slowly during the coldest months of the year.

8. The benthonic stage has very great possibilities of surviving under unfavourable conditions.

Polydora Bosc

The egg and sperm

The egg is of the thin-membraned type and lacks membrane vesicles. The sperm has a long head and a tapered acrosome.

Type of development

Fertilization is preceded by a copulation. The eggs are laid in capsules attached to the wall of the tube. Adelphophagia has been ascertained in two species (*Polydora hoplura* and *Polydora hermaphroditica*). During the pelagic stage the larvae are predominantly planktotrophic.

The pelagic larva

The form of the body differs considerably. The lateral parts of the peristomium are poorly demarcated from the prostomium. There are three pairs of black eyes, of which the most lateral are double-eyes (see page 155). Nuchal organs are formed as longitudinal ciliated grooves. The palpi become well developed. Nototrochs are found. The pygidium is rounded and lacks appendages. The telotroch is well developed. The pigmentation is vivid, and melanophores occur. The larval setae are relatively short. The adult bristles are developed early (exceptions: *Polydora antennata* and *Polydora pulchra*). In old larvae there are specialized bristles in segment 5. A "ciliated pit" is lacking (exception: *Polydora caulleryi*). Gastrotrochs occur in an irregular pattern.

Key to species

1. Short and thick larvae with regard to their length. A dorsal median melanophore is found on the posterior part of the prostomium, and one on the pygidium. 2.
   Slender larvae. Without median melanophor on the prostomium and on the pygidium. 3.
2. Four rows of dorsal, ramified melanophores in the segments. Yellow and green pigment (reflected light) is found. *Polydora pulchra* (p. 131).
   Only two rows of dorsal ramified melanophores. Yellow and green pigment is lacking. *Polydora antennata* (p. 126).
3. A dorsal median row of melanophores is found at least caudad of segment 5. 4.
   Without row of dorsal median melanophores. 5.
4. The dorsal median melanophores are abundantly ramified. *Polydora hermaphroditica* (p. 111).
   The dorsal median melanophores are not ramified but attached to a vesicular tissue. *Polydora coeca* (p. 120).
5. Pharynx and proctodaeum strongly pigmented. Melanophores first in the posterior third of the body. A "ciliated pit" is found. *Polydora caulleryi* (p. 123).
   Pharynx and proctodaeum unpigmented. Dorsal melanophores at least from segment 5 onwards. 6.
6. *One pair* of median melanophores in all segments. From segment 7 onwards a transverse row of star-shaped melanophores. *Polydora flava* (p. 117).
   Without pairs of median melanophores at least in the first two segments. Transverse rows of small star-shaped melanophores are lacking. 7.
7. The first five pairs of median melanophore are band-shaped, thereafter star-shaped. Ventrally yellow pigment collected in three longitudinal rows of chromatophores. *Polydora ligni* (p. 106).
   The first six to seven pairs of median melanophores are band-shaped, thereafter star-shaped. If yellow pigment occurs it is not concentrated in distinct chromatophores. *Polydora ciliata* (p. 101).

Polydora ciliata (Johnston)

Occurrence in the area of investigation

This species occurs abundantly in the area of investigation and is recovered from the most varying substrata. It is found boring in calcareous shells, e.g. subfossil *Ostrea* shells, in the apex of the shells of *Littorina littorea*, in the edge of the shells of *Patella vulgata*, etc., but is found also in *Lithothamnion*, in sand containing calcareous shellfragments, in the sponge *Halichondria panicea*, in the stalks of *Zostera*, and in mud composed chiefly of organic material etc. In the last-mentioned material it lives in very great numbers at depths of about 10–15 meters immediatly east of the Koljö island in the Koljö Fjord.

Occurrence in plankton

Polydora ciliata larvae appear in the Gullmar Fjord during two widely separated periods of the year. The most prolific spawning takes place around the beginning of March until the middle of June. The second spawning

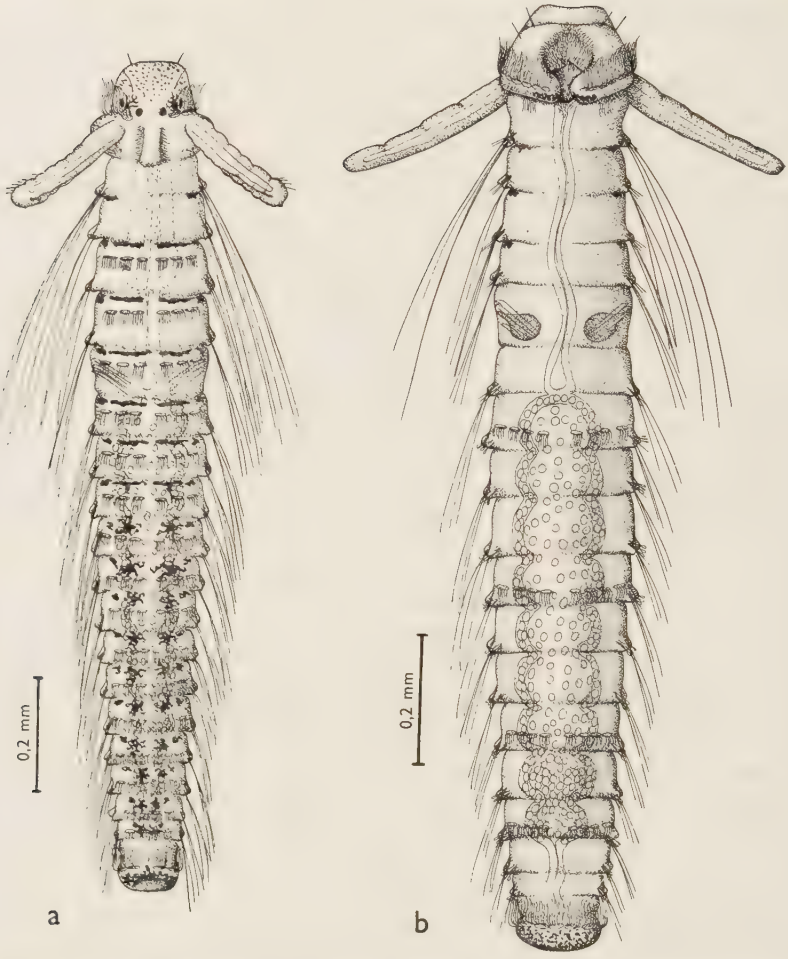


Fig. 35. *Polydora ciliata* (Johnston). a) Pelagic larva (dorsal view). b) Pelagic larva (ventral view).

begins at the end of September, and ends in December. During the spring spawning it is very easy to obtain egg-capsules with embryos, especially in subfossil *Ostrea* shells which are readily workable. In the autumn I have secured egg-capsules both from calcareous shells and from soft bottom specimens. Identical larvae are developed from either egg-capsules, and they agree with the spring larvae.

The pelagic larva (figs. 35a, b)

Since the entire development of this species is very well known (see Literature p. 106) it will not be included here for renewed description. A comparison between this larva and that of *Polydora ligni* is given on page 107.

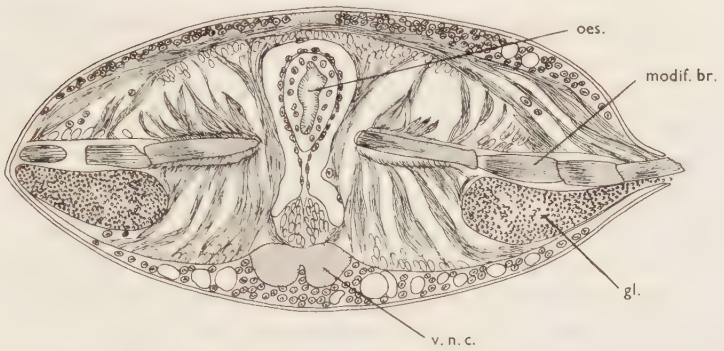


Fig. 36. *Polydora ciliata* (Johnston). Cross section of segment 5 of an old pelagic larva. oes. = oesophagus, modif. br. = modified bristles, gl. = gland with granular contents, v.n.c. = ventral nerv cord.

Glands in connection with the so-called bore-bristles in segment 5, and observations concerning the boring.

One detail which may be of some interest and which has previously escaped observation will, however, be treated here.

In larvae ready to metamorphose (17–20 segments) a pair of opaque gray structures, which have about the same length as the so-called bore-bristles (fig. 35b) can be observed in segment 5 ventrad to these bristles. On closer inspection it is found that they are each divided into several lobes. A cross section of this region of the body reveals that they are glands containing a granular secretion, and located in connection with the seta-sacs and open under the tips of these bristles (fig. 36). The granular contents of the glands are stained light red or brownish red with eosin and vermilion red with azan on Bouin-fixated material. In younger larvae the glands are composed of four to five retort-shaped glandular cells, which have very thin walls and a small nucleus lying pressed against the cell wall. The nucleus is very dense and is stained intensely blue with haematoxylin. In older larvae the cellular margins between the gland cells appear to disintegrate.

Claparède (1870) has described a kind of glands in *Polydora ciliata* consisting of 15–20 cells, which he called "poches glanduleuses". The gland cells lie concentrated in a circle and have fibrous contents, and each cell opens out separately on the surface of the epithelium. The apertures are likewise situated in a small circle ventrad and mediad to the neuropodium. There are two such glands in each segment. Such "poches glanduleuses" are found in the larva as well as in the adult stage of *Polydora ciliata* and others belonging to the subfamily *Spioninae*. In the larva ready to metamorphose of *Polydora ciliata* they are found in segments 7, 8, and 9, and are faintly stained with haematoxylin. Each gland consists here of about

four to five cells. These glands exhibit so great similarities in form and location with those in segment 5 that one can easily conceive them as homodynamic, in spite of the different composition of the secretion, etc. One might be able to think of the glands in segment 5 as "poches glanduleuses" specialized for a certain purpose. The connection with the so-called bore-bristles in segment 5 gives support to the idea that they secrete a substance which facilitates the boring of the worm. The described glands are reduced after the metamorphosis and should, therefore, be of importance only in the first penetration of the substratum. I have repeatedly had the opportunity of studying the boring of the metamorphosing larva. When it comes in contact with a piece of calcareous shell it relinguishes its swimming mode of life and begins to crawl over the shell (see p. 186). At the same time the form of the body undergoes a change. From having been fairly oval in cross section it now becomes flattened. A mucus trail is secreted. The movements are lively and energetic, and the palpi are borne directed anteriorly instead of downward-posteriorly as when swimming. When it has found a site where it can attempt to build its tube, i.e., a depression, one interstice between two lamellae in the shell, a deserted tube of a *Polydora*, etc., it stops crawling and begins to bore. At this time the tips of the so-called bore-bristles, which normally are directed toward the sides (fig. 36) are placed in ventral direction so as to be directed against the shell. Thereafter the bristles are forcibly lifted obliquely upward and outward. This movement is repeated in rapid succession. Before this occurs, however, it is probable that the larva has attached itself to the shell by means of secretion from its numerous ventral epithelial glands. Boring would be hardly conceivable otherwise, as the worm could not anchor itself on the smooth surface of the shell by means of its ventral crochets only. After about an hour the worm has surrounded itself with a tough hyaline tube, which is probably formed by its numerous dorsal unicellular epithelial glands. Since the tube rapidly becomes opaque the continued boring cannot be studied.

There are thus in my opinion many factors which indicate that the boring of the larvae involves both a chemical and a mechanical action on the material. Presumably a substance secreted by the described glands converts the lime into a more easily workable substance which is later eroded with the help of the bristles. Since the described glands are exclusively larval, it is conceivable that the boring in older individuals is accomplished entirely with the aid of the bristles.

Literature concerning the boring in Polydora ciliata

The literature on this subject is extensive. As early as c. 1670 Swammerdam in his "Biblia naturae" (published 1737) reported that he had observed

that the shells of *Littorina littorea* were pierced by a small worm. LANKASTER (1868) was the first to treat the actual boring of the species. He assumed that it took place by chemical means. He did not believe, on the other hand, that the bore-bristles could have any effect on the lime. He advanced the theory that the worm employed an acid secretion from the previously mentioned "poches glanduleuses". MCINTOSH (1868) could not, however, observe any acid reaction from the mentioned glands, and was of the opinion that the boring took place without chemical agents. This view was supported by his observation that the worm could bore in other substances than lime. WHITELEGGE (1888) studied *Polydora ciliata* in oyster banks in Australia. He favoured the view that *Polydora ciliata* actually did not bore at all. He thought instead that the young *Polydora* larvae attached themselves to the inside of the oyster shell and surrounded themselves there by a little tube of mud. Irritated by the worm the oyster should than begin to deposite a layer of lime over the animal. Presumably he did not know that the worm is found also in the apex of the shell of *Littorina littorea* or in subfossil shells. SÖDERSTRÖM (1920) also dealt with the boring of *Polydora ciliata*. He demonstrated that the U-shaped tube resulted from an originally undivided hole in which an intermediate wall of detritus, etc., was built up. With regard to the actual boring he considered it to be a joint effect of an acid, secreted from the "poches glanduleuses", and a mechanical action with the modified bristles in segment 5 (the "bore-bristles"). He supported this conception by direct observations on living material, and by staining experiments with neutral red, which showed that the "poches glanduleuses" were stained deep red. According to him, this proved that these secreted an acid product, which attacked the shells. He presumed this acidic product to be hydrochloric acid. In a later investigation (1923) he verified the occurrence of *Polydora ciliata* in so-called "Buntsandstein" on Heligoland. On this occasion he was able to show that this kind of rock contained approximately 20 per cent lime, and therefore the boring with the help of an acid is not contradicted by this finding. On the contrary, he was now inclined to lay less emphasis on the mechanical boring of the worm. He considered that the so-called bore-bristles had their importance as adhesive organs. In regard to SÖDERSTRÖM's theories on the secretion of the "poches glanduleuses", it must be said that these glands in all probability secrete a mucous substance. This is indicated by staining with azan, with iodine green, and with hematoxylin. Mucus has a weakly acid reaction, but I do not think that it can be of any great importance as a lime-solvent. That the so-called bore-bristles should be primarly adhesive organs, as believed by SÖDERSTRÖM, is not supported by my direct observations. A person who has otherwise seen in section the enormously strong muscles which move these bristles (fig. 36) finds it difficult to think that these should have been

developed only for pressing the bristles against the wall of the tube for the purpose of adhering.

Literature concerning the development

The larval development of this species has been treated in several papers. I shall not give a complete report of this literature here but only mention some of the more important works. The first description of the pelagic *Polydora* larva was given by Örsted (1843). He classified this larva under *Leucodorum ciliatum* Johnston which is synonymous with *Polydora ciliata* (Johnston). Frey and Leuckart (1847) treated a larva which agreed in important points with that of *Polydora ciliata*. They referred it to *Lecodorum paradoxum* which species can also be synonymous with *Polydora ciliata*. The larva described by Claparède (1863) as belonging to this species is not a *Polydora ciliata* as has been demonstrated by several investigators. Casanova (1952) found that it belonged instead to *Polydora antennata*. (Independently of Casanova I had found in 1948 that this larva belongs to a variety of the species, namely var. *pulchra* Carazzi, which in this work has been set up as an independent species. See p. 126.) Mecznikow (1865) examined the egg-capsules for the first time. Among other investigators who have treated the pelagic larva may be mentioned Agassiz (1867), Mesnil (1896), and Leschke (1903). Söderström (1920) advanced a theory for the mode of formation of the egg-capsules. Wilson (1928) gave a complete and altogether excellent account of the development of the species, and showed that the larvae remained in the egg-capsules until they had attained the 3-segment stage. Thorson (1946) has described a *Polydora ciliata* larva. Strangely enough, he has not described any larva which he has classified as *Polydora ligni*. As the larvae of *P. ciliata* and *P. ligni* are similar it is conceivable that the latter has been overlooked.

Polydora ligni Webster

Occurrence in the area of investigation

This species occurs in several types of substratum. I have found it between the lamellae of subfossil *Ostrea* shells, in *Halichondria panicea*, and in different types of sand or muddy sand.

Occurrence in plankton

In contrast to the foregoing species this one occurs in plankton during only one period of the year, viz., from the end of July to the end of October.

General characteristics of the pelagic larva

This larva resembles the foregoing with which it agrees in size. It is, however, distinctly separated from it. In the following table the larvae are compared.

	P. ciliata	*P. ligni*
1)	The median eyes are round.	The median eyes are oval, somewhat obliquely placed.
2)	The number of band-shaped dorsal melanophores is 6–7.	The number of band-shaped dorsal melanophores is 4–5.
3)	The pygidium is always strongly pigmented black.	The pygidium is not always pigmented black.
4)	Ventral yellow pigment occurs only in the autumn larvae, but is never concentrated in distinct chromatophores.	Ventral yellow pigment is strongly developed, and concentrated in 3 ventral rows of chromatophores.
5)	Occurs in plankton in the periods March–June and September–December.	Occurs in plankton in the period July–October.

The larva ready to metamorphose (fig. 37 a)

A larva with 18 segments is chosen as typical of the stage.

The prostomium is rounded and somewhat notched at the tip. Between the innermost and the next to innermost pair of eyes there is an abundantly ramified melanophore. The median eyes are oval and somewhat obliquely placed. The palpi are well developed. Anterior to the palpi the prototroch extends to the level of the median pair of eyes. Other ciliation is found terminally in the form of a pair of relatively short tactile cilia, and anterior to the eyes there is another, somewhat longer pair. The nuchal organs reach hardly to the boundary between segments 1 and 2. The nuchal crest is weak. The parapodia have well-developed dorsal and ventral cirri, except in segment 5. The ventral cirri decrease in length posteriorly. Six pairs of branchiae occur from segment 7 onwards. Nototrochs are observed from segment 3 onwards, and consist each of six ciliated cells in single series. "Grasping ciliae" and intersegmental ciliation are found. The pygidium has a dorsal notch. It is provided with sensory cilia. Four dorsal rows of melanophores are found on the body segments. The lateral melanophores occur from segment 2 to segment 18 and are situated in the anterior part of the segments. They are most strongly defined in the anterior segments, but are lacking in segment 5. The median melanophores occur in segment 3 and the succeeding segments. Up to and including segment 6 they are band-shaped (i.e. four pairs of this type), and thereafter more or less starshaped. The lateral parts of the peristomium and pygidium may be pigmented black. Ventral of the modified bristles in segment 5 there occur glands of the same type as in *Polydora ciliata* (see p. 103). The larval setae are relatively short and iridescent. In segment 5 larval bristles are lacking. Adult bristles of the same type as those found in the adult stage are found. A "ciliated pit" is lacking, and gastrotrochs are found in segments 5, 7, 10,

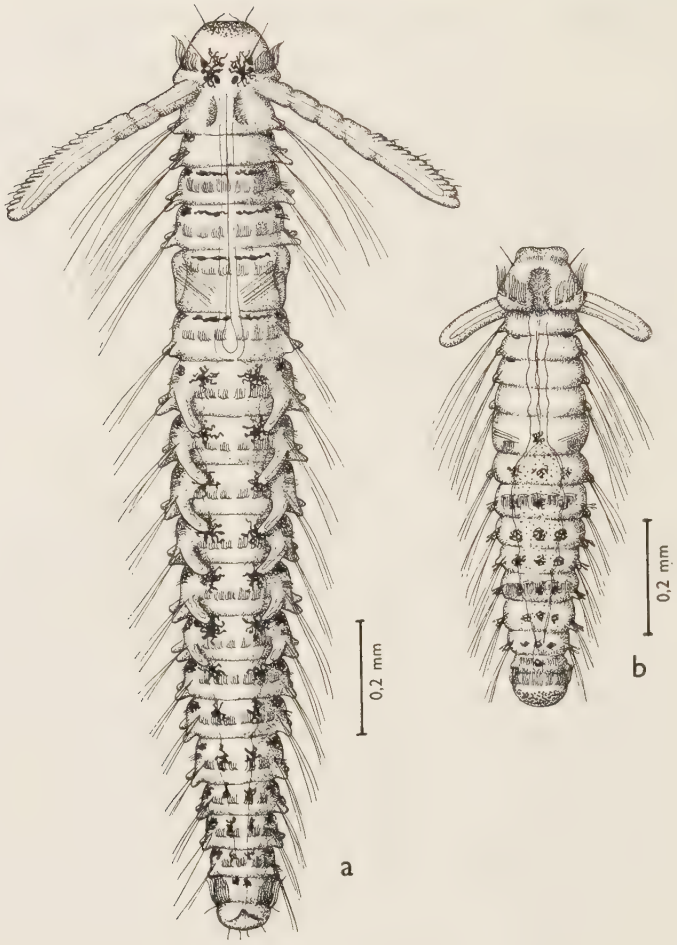


Fig. 37. *Polydora ligni* Webster. a) Larva ready to metamorphose (dorsal view). b) Young larva (ventral view).

13, and 15. An intensively yellowish-green pigment (reflected light) is observed ventrally. It occurs in the posterior two-thirds of the larva and is divided into three rows of chromatophores (fig. 37 b). I have observed a similar pigment in the autumn larva of *Polydora ciliata*, but is diffusely scattered, not concentrated in chromatophores.

The young benthonic stage (figs. 38 a–c)

The description is based primarly on one specimen with 23 segments and a length of 2.34 mm examined 11 days after the metamorphosis, and another specimen with 33 segments and a length of 4.10 mm examined 35 days after the metamorphosis.

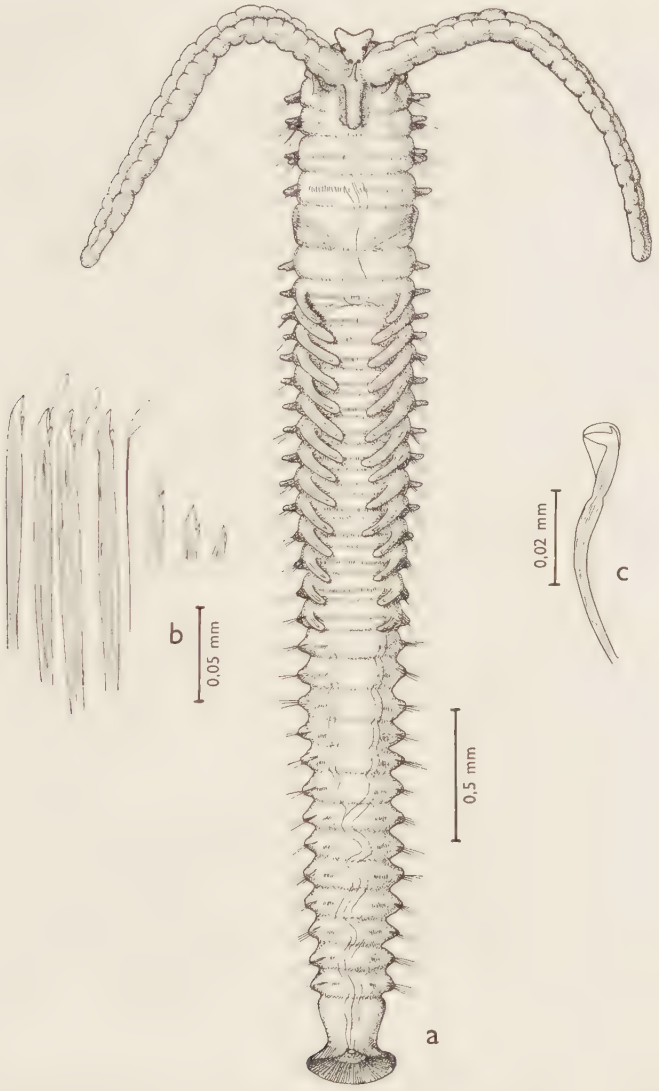


Fig. 38. *Polydora ligni* Webster. a) Young bottom stage (dorsal view). b) Modified bristles from segment 5 of the same. c) Ventral hooded crochet from the same.

The prostomium has been broadened at the tip, and has acquired a semicircular notch. A long and slender occipital tentacle has developed from the "crest". The ramified melanophores in the ocular region have been eliminated. The palpi have grown appreciably. The nuchal organs have been extended more posteriorly, but remain parallel. The nototrochs have been partly eliminated except in the branchial region. The pygidium has developed markedly and acquired the outspread form characteristic of the species.

The ventral cirri in segments 1 and 2 are long and slender, but decrease in length in the succeeding segments. The dorsal cirrus in segment 1 is directed upwards, in the succeeding segments, however, outwards. Branchiae occur from segment 7 onwards in a varying number according to the size of the animal. (An individual with 49 segments had 23 pairs). The oesophagus is somewhat convoluted and extends through segment 9. The stomach exhibits distinct segmental diverticula and merges into a convoluted rectum in the last segments. The adult bristles show great similarities to those found in *Polydora ciliata*. There are, however, certain differences. Segment 1 has ventral, but no dorsal hairy bristles. The modified bristles of segment 5 are of the same type as those encountered in *Polydora ciliata*, but differ by having a somewhat straighter tip (fig. 38b), a characteristic which I have found common to a large number of specimens. Ventral crochets are found from segment 7 onwards (fig. 38c). In the recently metamorphosed worm there are only four to five in each neuropodium. In a two-month-old specimen with 49 segments there were 12 per neuropodium (compared with 7 in *P. ciliata*).

Identity of species

The typical formation of the prostomium with an occipital tentacle, the outspread pygidium, and the large number of crochets per segment eliminate other species.

Biology of the benthonic stage

The metamorphosis in this species is very slightly dependent upon a specific substratum. Metamorphosis has been obtained in pure sand, on fragments of subfossil *Ostrea* shells, etc. In sand irregular tubes are built of mineral grains and a secretion. Sand particles are lifted up by means of the palpi to a cone at the mouth of the tube. The worm consumes detritus, plankton, etc.

Literature

Söderström (1920) described the egg-capsules, which differ from those of *Polydora ciliata* by being attached to the wall of the female's tube with two processes compared to one in the latter, and in that the individual capsules are free from each other. In *P. ciliata* they are connected in a row. The larvae described by Hofker (1920) as *P. ciliata* probably belong to *P. ligni*. They have, namely, five pairs of bandshaped melanophores, and relatively straight-tipped "bore-bristles". Hartman's (1941) *P. ligni* larva must, however, probably be referred to *P. ciliata*. This classification is supported by its seven pairs of band-shaped dorsal melanophores. Smidt (1951) found in his area of investigation (western Denmark, "Waddensea")

adult *Polydora ligni*, but only larvae which he found to agree completely with those of *Polydora ciliata* as described by Leschke (1903), Wilson (1928), and Thorson (1946). On the basis of his findings he advanced the theory that *Polydora ciliata* and *Polydora ligni* should constitute one and the same species with a certain degree of variation. He figured, however, a larva with five pairs of band-shaped melanophores, and this one at least is probably a *Polydora ligni* larva.

I am convinced that we are dealing in this case with two well-defined species, which do not bastardize. I have never observed either a larva or an adult exhibiting transitional characteristics between the two species. It is, however, indisputable that they are fairly closely related.

Polydora hermaphroditica n. sp.

Occurrence in plankton

The larva is encountered from the end of July and occurs in isolated specimens until the beginning of December. At times it is found in very great numbers.

Size and general characteristics of the pelagic larva

Due to the fact that the larva often contracts greatly when placed between the object-glass and the cover-glass the following measurements must be considered as very approximate.

Segments	Length mm	Width mm
11	0.82	0.18
14	1.05	0.22
17	1.40	0.28
22	1.60	0.36

The larva is characterized by its considerable size, lateral yellowish-brown pigmentation on the prostomium, and by the dorsal median rows of melanophores from segment 6 onwards.

The big pelagic larva (figs. 39a–d)

The prostomium is rounded and bears on the anterior side a number of verrucae of the same type as found in larvae of *Polydora flava* (p. 117). The nuchal crest extends posteriorly through segment 1. The upper side of the prostomium is provided with tactile cilia. A pair of these is attached anterior to the lateral pair of eyes, and one pair anterior to the median pair. There are three pairs of black eyes. Between pairs 1 and 2, counted

from the median line, there is an abundantly ramified melanophore. The prototroch lacks tactile cilia. The nuchal organs are very strongly developed, more so than in any other Spionid larva I have observed. They are S-shaped and run with their anterior shanks laterally on the anterior side of segment 1. The ciliation is remarkably well developed.

All segments except the fifth have both dorsal and ventral cirri. The dorsal cirri are very small, but the ventral cirri are better developed. In the largest pelagic larvae there are small branchial anlages from segment 7 onwards. From segment 3 onwards are found well-developed nototrochs. "Grasping cilia" are found from the middle part of the body onwards. The pygidium is cylindrical with a notch.

There is a yellowish-brown pigmentation ventral of the basis of the palpi, and also on the pygidium. The dorsal melanin pigmentation consists of two systems: 1) Laterally on the anterior side of each segment beginning with the second there is a small unramified pigment spot in the anterior two-thirds of the body. 2) Along the median line of the animal there is a row of melanophores, which in segments 2 4 are band-shaped, but in the following segments more or less star-shaped. There is also a suggestion of black pigment on the pygidium.

The oesophagus, which like the pharynx is unpigmented, extends to about segment 5. The stomach has a whitish colour with a somewhat greenish tinge, and is thick-walled. The wall contains numerous oil drops. There is no differentiated proctodeum.

The larval setae are short and lustreless. Adult ventral and dorsal hairy bristles are found. The modified bristles in segment 5 are of the same type as is encountered in larvae of *Polydora ciliata*. In one of the two types the tip is somewhat curved and a small lateral serration is observed. The other type, which is somewhat larger, lacks a lateral serration and has, remarkably enough, a slit-shaped opening in its interior. Finally, there is a strong bristle with the exterior part greatly narrowed and S-curved. The modified bristles are accompanied by thin hairy bristles (fig. 39c). From segment 7 onwards there are found ventral crochets, three to five in each neuropodium. They are diserrated (the serrations form a comparatively small angle with each other), and have manubrial thickening. They are accompanied by a number of long "winged" hairy bristles. The entire bristle equipment is very similar to that found in young individuals of *Polydora ciliata*.

Like the larvae of *Polydora ciliata* and *Polydora ligni* these have in connection with the modified bristles in segment 5 glands with granular secretion (cf. p. 103).

The ventral side of the prostomium is richly ciliated. The prototroch runs laterally down on the lateral lips of the vestibule. Neurotrochs and a "ciliated pit" are lacking. Gastrotrochs are found in segments 3, 5, 7,

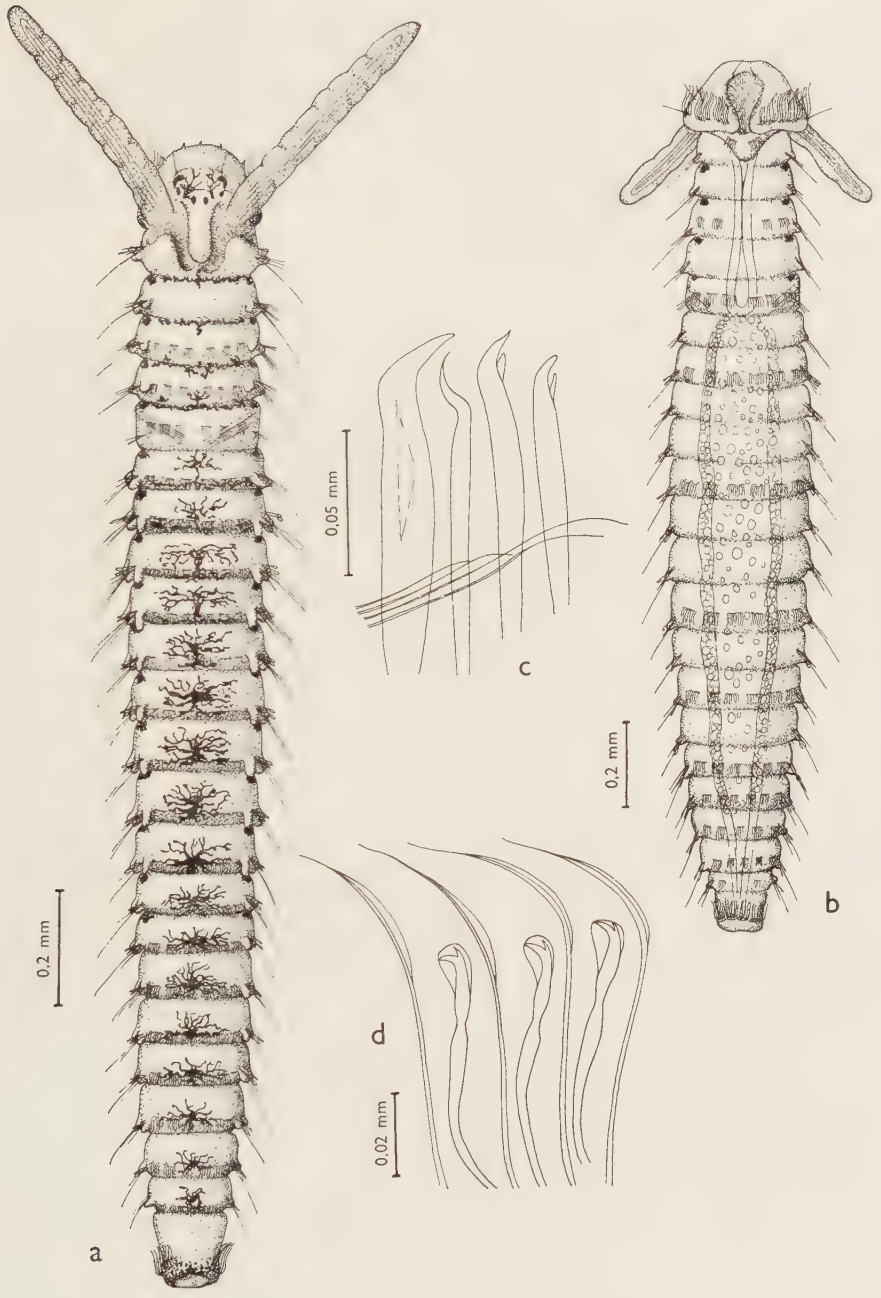


Fig. 39. *Polydora hermaphroditica n. sp.* a) Big pelagic larva (dorsal view). b) Big pelagic larva (ventral view). c) Bristles from segment 5 of a big pelagic larva. d) Ventral bristles from hind segment of the same.

10, 13, 15, 17, 18, 19, etc. Black pigment runs ventrally down between segments 1 and 2, 2 and 3, 3 and 4, 4 and 5.

All the larvae examined (a total of about 100) either lacked sexual products or had male products. The largest of all continued active sperm. No female sexual products, on the other hand, have ever been observed. We have thus here an example of male neoteny. This has not been observed previously in any polychaete larva.

The young benthonic stage

In cultures it is very difficult to induce metamorphosis in this larva. I have, however, succeeded in getting a small number of specimens, only six in all, to do this. The breeding was went on from October 10, 1953 to March 25, 1954. The specimens were of varying size. The largest had a length of 15.5 mm and 65 segments. They were found to agree in almost all characteristics with *Polydora ciliata*. The prostomium is extended and slightly notched at the tip. Its lateral sides are parallel. There are two pairs of black eyes. The palpi are long and well developed. The nuchal crest extends posteriorly halfway through segment 2. The nuchal organs are considerably less strongly developed than in the larva, both relatively and absolutely. Dorsal and ventral cirri are found in all segments except the fifth. In segment 1 the dorsal cirri are drawn high up towards the median line, and directed upwards. Branchiae and nototrochs occur from segment 7 onwards. — Ventral "poches glanduleuses" (c. f. p. 103) are observed from segment 6 onwards. In segment 1 there are no dorsal hairy bristles, but in the succeeding segments they are found both notopodially and neuropodially. The modified bristles in segment 5 are of the same type as those encountered in *Polydora ciliata*. Ventral crochets occur from segment 7 onwards, and have the same appearance as those in *Polydora ciliata*. In contrast to this species there exist, however, up to 11 per segment. In the posterior notopodia no bristles of divergent type are observed. All are long, straight hairy bristles (winged). The pygidium has developed the funnel-shaped structure which is characteristic of many *Polydora* species. The pharynx extends through segment 2, the oesophagus through segment 13. A proctodeum has been differentiated in the last seven segments. In each of the egg-capsules of the last-mentioned individual there were 4–7 embryos and 20–26 abortive eggs. The embryos had suggestions of two segments, and one pair of black eyes. Unfortunately time did not permit breeding of these larvae, which judging from all findings have a very long life under parental care.

This species thus exhibits a very peculiar form of protandry and neoteny. The larvae always develop male sexual products which are resorbed during

Sexual phases of the benthonic specimens

Segments	Sperms in segm.	Eggs and oocytes in segm.	Spermatophores etc.
22	—	—	—
34	—	—	—
39	7–15	—	—
47	7–16	17–40	?
56	Very few in segm. 7–16	17–40	Spermatophores in receptacula seminis
65	7–19	20–40 ?	Had 16 egg-capsules

the first benthonic stage. At the 40-segment stage sperms are again formed in segments 7–15 (19). During the 45 50-segment stage femal sexual products are then formed from segment 17 posteriorly. That a copulation with concomitant fertilization takes place is shown partly by the fact that one of the individuals had spermatophores with active sperms in the dorsal receptacula seminis in segment 34 and in the following segments, and partly by the fact that one individual, which had grown more rapidly than the others, had developed egg-capsules containing living embryos. This is also the first time that spermatophores have been ascertained in the genus *Polydora*.

The interpretation of these two sexual phases through which every individual passes, viz., a male neotenic larva and hermaphroditic adult, is very difficult. To judge from the observations there exist larvae of two different developmental types. One of these, that which develops into the neotenic male, has a long pelagic stage, and the period of brood protection is presumably short or of moderate duration. The other type should be represented by the embryos I have observed in the previously mentioned egg-capsules. To judge from the great quantities of abortive eggs these embryos probably develop directly (cf. *Pygospio elegans*, p. 97), or also have a very brief pelagic stage. It is conceivable that this larval type develops into males and females, which give rise to the neotenic larval type. The neoteny cannot, however, be explained by this reasoning. Perhaps still another developmental type is involved (cf. *Dodecaceria concharum*, Caullery and Mesnil 1898). Further studies of these interesting problems are desirable.

Biology

It is very difficult to get this larva to metamorphose. Innumerable attempts have been carried out under varying conditions. A series of different bottom substrata have been tried, e.g., different kinds of lime substrata (*Lithothamnion*, subfossil *Ostrea* shells, living mollusks, etc.), different kinds

of sand (shell sand, mineral sand, sand mixed with mud, etc.), different kinds of mud, different kinds of living plants as *Zostera*, *Fucus*, etc., but none of these have proved inductive to metamorphosis. The larva has one stage when it partially loses its larvals organs, as for example, the larval setae, and during this stage it is alternately swimming and crawling. This can continue for a very long time, up to one month. In the vast majority of cases the larvae subsequently died. In the successful experiment no form of bottom substratum was employed. By means of a special arrangement (Hannerz 1953), however, the water in the culture bowls was kept in constant circulation. This seems to have been of great importance for the metamorphosis. In this culture the larvae could, namely, give up their swimming-crawling mode of life and settle down on the walls of the bowl, where they completed hyaline tubes to which were attached fecal balls, etc. The only food taken up was *Nitzschia*.

In the beginning the culture bowl was kept on an aquarium table with running water where its temperature could be maintained at about 8–10°C. Up to this time, as far as could be judged, no sexual products had started to develop in the coelom or at most in a very insignificant degree. From the middle of January 1954 the temperature, however, was raised to about 19°C. Immediately thereafter sexual products began to be developed in some specimens so that they were faintly visible through the body wall.

Identity of species

From the foregoing description of the benthonic stage it is evident that as a newly described species this is very similar to *Polydora ciliata*. There is no doubt, however, that it must be regarded as separated from the latter. In *Polydora ciliata* there occur usually five to seven ventral hooded crochets per neuropodium, exceptionally eight to nine may be observed. In this species, however, up to eleven are developed. There are, moreover, great differences in regard to the larvae. Still another *Polydora* species has been described as hermaphroditic, namely, *Polydora Giardi* (Mesnil 1896). From this species *Polydora hermaphroditica* n.sp. differs in a very important property. Branchiae occur, namely, in the last-mentioned species from segment 7 onwards, in *Polydora Giardi* more posteriorly.

Literature

Gravely (1909 B, pp. 48–50, pl. II, 28–30) described a larva which he called "*Polydora A*". This larva agrees with that of *Polydora hermaphroditica* in regard to the appearance of the nuchal organs, the location of the gastrotrochs, the dorsal pigmentation, etc. Furthermore, Gravely found: "... In both these larvae and in all others of sufficient age, a number of segments increasing with the growth of the body and commencing with segment 9,

contains a deeply stained granular substance which in balsam preparations of whole specimens stained with borax-carmin, closely resembles developing spermatozoa." There cannot be any other doubt of GRAVELY's "*Polydora A*" being identical with the larva of *Polydora hermaphroditica*.

HÄCKER (1898, p. 17, Pl. II, figs. 17–18) gave an account of an unidentified larva, which probably should also be referred to this species.

Polydora flava Claparède

Occurrence in the area of investigation

I have found this species in *Lithothamnion* crusts from the shoal Smedjan west of the island Flatholmen.

Occurrence in plankton

The larva has been encountered in plankton from the middle of July until the end of November. It never occurs in abundance.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
15	1.20	0.22
18	1.50	0.24

The larva is characterized mainly by its spool-shape, which is caused by the fact that the "head" and the pygidium are relatively small, by the green pigmentation on the prostomium and pygidium, and by the characteristic pattern of the melanin on the dorsal side.

The larva ready to metamorphose (figs. 40a–c)

A larva with 18 segments is chosen as a typical specimen. The prostomium is bluntly rounded and lacks tactile cilia. It is provided with a number of anteriorly directed tapered verrucae. The nuchal crest extends posteriorly through segment 1. Three pairs of black eyes are located in a straight line. The lateral ones coincide when seen from above. The prototroch is fairly weak and lacks tactile cilia. The parapodia remain relatively undifferentiated. Cirri are lacking in segment 5. Branchiae occur in the segments 8–10. Nototrochs are found from segment 2 onwards. The pygidium is rounded and has a well-developed telotroch. The dorsal melanin pigmentation is characteristic. Laterally on each segment there is a melanophore on the anterior side of the parapodium. Furthermore, there are a pair of transversally extended melanophores medially in all segments (even the first). Anterior

to these from segment 7 there is a band of smaller star-shaped melanophores in each segment. The prostomium and pygidium have a pretty green colour. The oesophagus extends through segment 7, where it merges into a stomach with abundant oil drops in the walls. The larval setae are short and strongly iridescent in reflected light. The following adult bristles are found: Hairy bristles dorsally and ventrally in all segments. Modified bristles in segment 5. They resemble those of *Polydora ciliata*, but lack lateral serration. They are accompanied by a number of smaller bristles (fig. 40c). Diserrated crochets appear from segment 7 onwards (fig. 40e). They lack manubrial swelling, and the angle between the serrations is relatively small. Dorsally in the posterior part of the body there are anlages to bundles of thin capillary bristles, which are typical for the species. On the under side of the prostomium, immediately anterior to the peristomium, there is a row of cilia which are longer than those in the vestibule. The prototroch extends ventrally on the lateral lips as far as to the vestibule. Here there is also a pair of long tactile cilia, which are ventrally directed. The neurotroch opens in segment 2 into a depression, which can possibly be interpreted as a simplified "ciliated pit". Gastrotrochs are found in segments 3, 5, 7, 10, 13, 15, etc. The foremost gastrotrochs are represented by only one pair of lateral ciliated cells, the following one by four, and thereafter by seven. On the ventral side of the posterior part of the body there is diffuse yellow pigment.

The young bottom stage

The description is based chiefly upon an individual with 26 segments. The prostomium has been markedly extended, and has acquired a terminal notch. The nuchal crest, which is fairly broad, extends a distance into segment 3. The nuchal organs are parallel. The palpi have grown considerably, but are relatively slender. Dorsal and ventral cirri are found in all parapodia. They decrease posteriorly in length. There are still no branchiae in segment 7, but they occur in the succeeding segments. They are longest in segment 9. Nototrochs occur only in the branchial segments. The pygidium is fairly thick and of the same type as in *Polydora ciliata*, i.e., a "funnel" with a dorsal notch. The larval pigmentation is unchanged. A pharynx has been differentiated. The oesophagus is very long and extends through segment 13, where it passes over into the stomach. A slightly convoluted rectum has been differentiated. Dorsal and ventral hairy bristles are found in all segments (thus even in the first). The modified bristles in segment 5 are accompanied by lanceolate bristles and are identical with those encountered in the larva ready to metamorphose (fig. 40c). Ventral crochets are found from segment 7, three to four per neuropodium, and of the same type as in the larva (fig. 40e). The fine capillary bristles, in dorsal bundles which were already observed in the larva, are more numerous here.

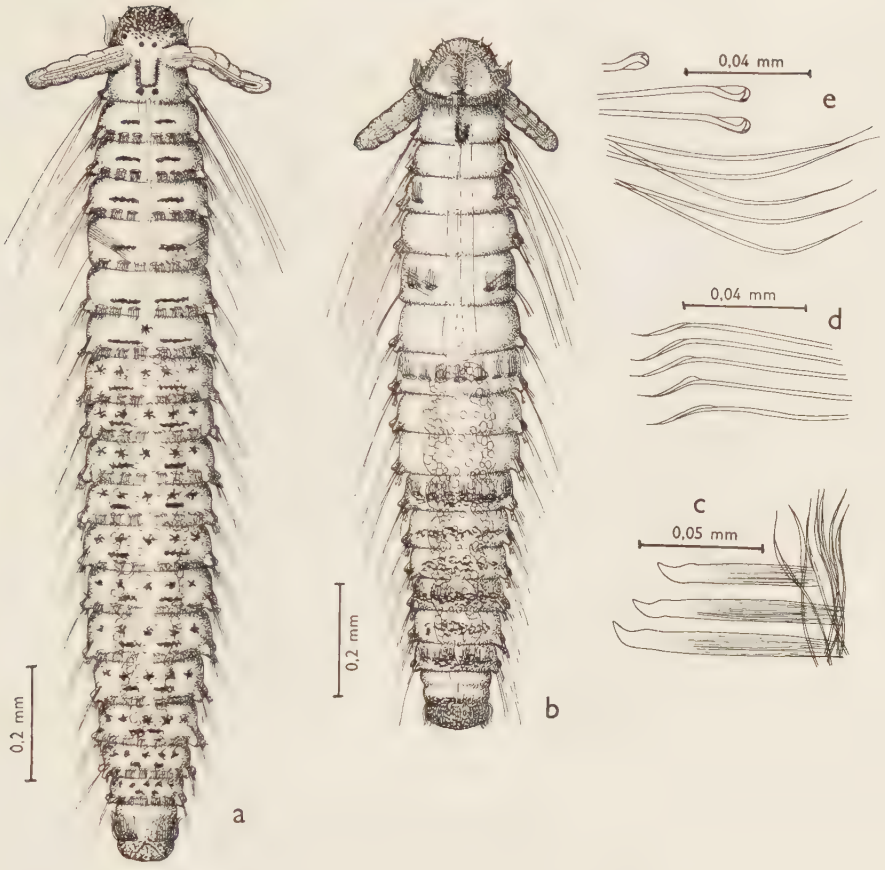


Fig. 40. *Polydora flava* Claparède. a) Larva ready to metamorphose (dorsal view). b) Somewhat younger larva (ventral view). c) Bristles from segment 5 of the same. d) Ventral "winged" bristles from segment 7 of the same. e) Ventral bristles from hind segment of a big larva.

Identity of species

The identity of the species must be considered established by the occurrence of the branchiae from segments 8–9, by the appearance of the ventral hooded crochets and of the modified bristles, and by the occurrence of dorsal bundles of fine capillary bristles dorsally in the posterior part of the body.

Biology

The metamorphosis is very dependent upon a specific bottom substratum. It can only be induced by *Lithothamnion* crusts. The worm seeks out fissures in these and there builds hyaline tubes, which extend a little above the surface of the crusts.

Literature

Häcker (1898, p. 17, pl. II, fig. 16) described an unidentified larva, which is possibly identical with this one as well as perhaps Gravely's (1909 B, p. 50, pl. II, fig. 32) "Polydora B".

Polydora coeca (Oersted)

Occurrence in the area of investigation

The species is earlier known from the area of investigation (Molander 1930). I have found it in sand at a depth of about 10 m immediately north of the island Långholmen.

Occurrence in plankton

The larva is encountered in plankton from the beginning of March to the end of April, and at times occurs in very great numbers.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
15	1.11	0.18–0.20
18	1.65	0.25

The measurements are very approximate, as this larva has a very great inclination to contract when placed between object-glass and cover-glass. When stretched out the largest larvae are considerably more than 2 mm long. The intensive yellowish-green colour on the prostomium and the pygidium, and the dorsal median row of melanophores in connection with a vesicular tissue are otherwise characteristic of the larva.

The larva ready to metamorphose (figs. 41 a, b)

Two larvae with 16–18 segments are chosen as typical of this stage.

The prostomium is rounded and somewhat notched terminally. It bears two (occasionally several) anteriorly directed cilia and three pairs of eyes. The palpi are fairly insignificant. The prototroch is robust and provided with interspersed tactile cilia. Nuchal organs have been formed. The parapodial cirri are weakly developed. Nototrochs are found from segment 2 onwards. The pygidium is bluntly rounded, dorsally somewhat notched, and bears a robust telotroch. The dorsal melanin pigmentation comprises three systems. Laterally on the anterior side of each segment there is a melanophore, in the anterior part of each segment there is a melanin band running across the body, which in the posterior segments is divided into

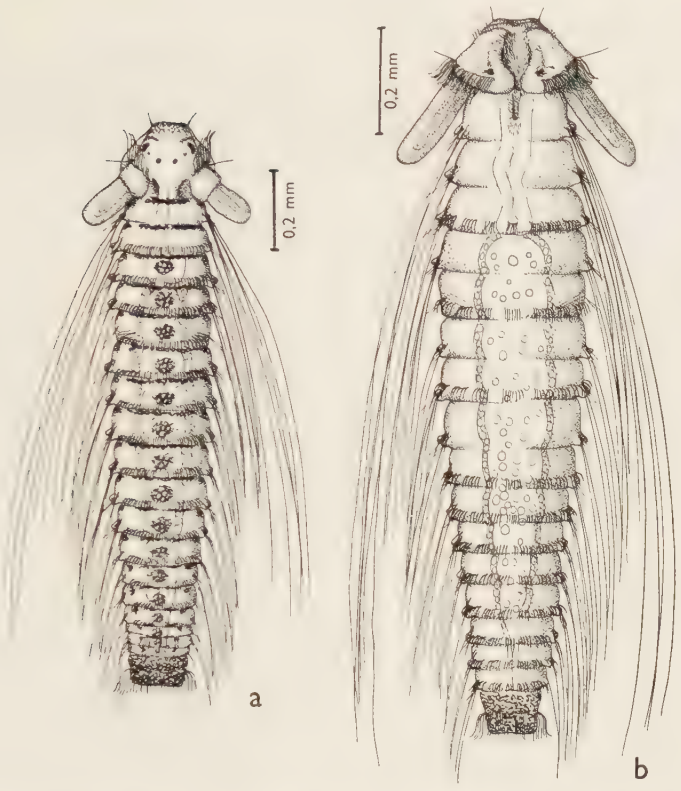


Fig. 41. *Polydora coeca* (Oersted). a) Big pelagic larva (dorsal view). b) Big pelagic larva (ventral view).

two and, finally, from segment 3 onwards a median concentration of melanin, which surrounds a number of blister-shaped unpigmented cells. The oesophagus extends posteriorly through segment 3, where it merges into a thick-walled stomach. No distinct rectum has yet been differentiated. The larval setae are long and irridescent. Dorsal and ventral adult hairy bristles are observed. They are smooth and somewhat curved. In the posterior segments ventral hooded crochets have been formed. The prototroch runs ventrally down to the vestibule. The lateral lips are relatively weakly ciliated. In the prototroch there are a number of interspersed tactile cilia. In segment 1 the neurotroch runs down into a shallow ciliated groove, which presumably may be regarded as a poorly developed "ciliated pit". In this respect the larva agrees with that of *Polydora flava*. Gastrotrochs occur in segments 3, 5, 7, 9, and all following segments. The median ciliated cells in the gastrotrochs are somewhat separated from the others. Ventrally pigment is lacking except in the prostomium and pygidium.

The young benthonic stage (figs. 42a–c)

The description is based chiefly on one individual with 28 segments and a length of 2.1 mm examined 14 days after the metamorphosis.

The prostomium has a terminal notch and lateral rounded lobes. One pair of eyes has been reduced. The palpi have grown and attained a considerable length. In the parapodia only the dorsal cirri are well developed. Distinct ventral cirri are found only in segments 2, 3, and 4. In segment 5 cirri are lacking. Branchiae occur from segment 8 onwards. Nototrochs, on the other hand, are found from segment 7 onwards. The pygidium has developed into a funnel-shaped structure, which is dorsally notched. The dorsal black pigmentation is undergoing reduction, but the prostomium and the pygidium retain their green colour. Both dorsal and ventral hairy bristles are found. Ventral crochets are observed from segment 7 onwards. They are diserrated and do not have manubrial swellings (fig. 42c). In segment 5 strong modified bristles have been developed (fig. 42b).

Identity of species

The only species with which a confusion is conceivable is *Polydora flava*. Both these species have in segment 5 modified bristles of the *Polydora ciliata* type but without lateral serrations, and ventral crochets without thickened manubria and where the serrations form a relatively small angle with each other. *Polydora flava* has, however, dorsal bundles of fine bristles in the posterior part of the body (cf. p. 118). Since such bristles are lacking here, and since I have identified the larva of *Polydora flava* this one should belong to *Polydora coeca*.

Biology

The metamorphosis is readily induced by *Lithothamnion*. It is, however, not so substratum-specific as in the foregoing species. On several occasions I have obtained metamorphosis in clean glass bowls without substratum.

Literature

Thorson (1946, p. 90, fig. 43) described a larva which he presumed belonged to *Polydora coeca*, as this and the larva are common in Öresund. The larva described here agrees well with his.

Polydora quadrilobata Jakobi

Occurrence in the area of investigation

I have obtained a number of specimens of this species from the sound between Blåbergsholmen and Kristineberg at a depth of about 1 m in muddy sand.

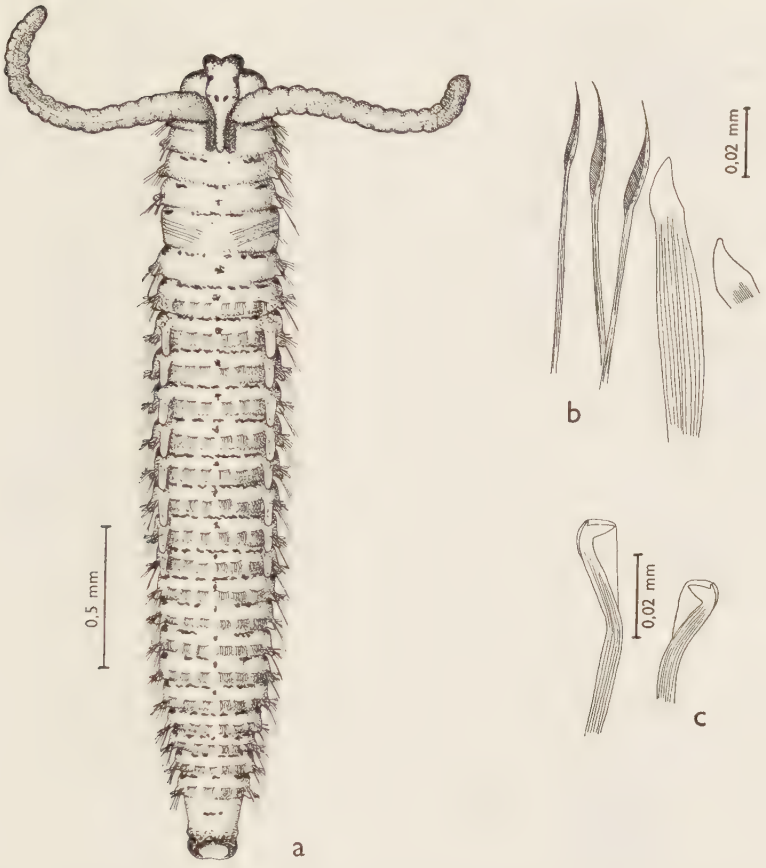


Fig. 42. *Polydora coeca* (Oersted). a) Young bottom stage. b) Bristles from segment 5 of the same. c) Ventral hooded crochets from the same.

Pelagic larva

I do not know of any larva which can conceivably be referred to this species.

Literature

Jakobi (1883) reported that the development like that of *Polydora ciliata* takes place in egg-capsules, and also mentioned the pelagic larva, but did not describe it.

Polydora caulleryi Mesnil

Occurrence in the area of investigation

I have found one specimen of this species in a subfossil *Cyprina*-shell, markedly affected by *Cliona*, from the Gåsö channel west of the island Skaftön.

Occurrence in plankton

The species occurs in plankton from the end of February until the end of April. It has been obtained on February 20 at the earliest (1952) and latest on April 25 (1951). It is very abundant at times.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
11	0.80	0.18
13	1.20	0.21
20	2.20	0.39

The larva is characterized primarily by the deeply black-pigmented pharynx and hind part of the rectum, the vivid green colour in the prostomium and pygidium, and band-shaped melanophores, which occur only in the posterior third of the body.

The larva ready to metamorphose (figs. 43a, b)

Larvae of the 12–13-segment stage are chosen as typical specimens.

The prostomium is stumpy and somewhat notched terminaly. There are three pairs of black eyes. The prostomium is richly set with tactile cilia. The prototroch is well developed and provided with interspersed tactile cilia. The palpi are well developed and attached by palpophores, which arise from the lateral parts of the peristomium. The nuchal organs are well developed. Both dorsal and ventral cirri occur in the parapodia of all segments. Nototrochs are found from segment 2 onwards. They consist of four ciliated cells each. The pygidium has the form of a rounded "knob" with a dorsal notch. The telotroch is well developed. The prostomium and pygidium are pigmented green. Melanin occurs very sparsely in the epidermis. From segment 7 onwards, however, there is a pair of band-shaped melanophores in each segment. The pygidium has dorsal melanin streaks. The inside of the "pharynx" is richly pigmented with melanin and extends through segment 2, where it merges into the stomach, which is thick-walled and provided with segmental diverticula. The gut near the anus is pigmented black. The larval setae are long and relatively thin. Of adult bristles there are hairy bristles and anlages to modified bristles in segment 5. The prototroch runs down on the lateral lips. In addition to the fine ciliation of the vestibule there is a number of tactile cilia. In segment 1 a broad neurotroch is observed which in segment 2 runs into a "ciliated pit". Gastrotrochs occur in segments 3, 5, 7, 10, and 12.

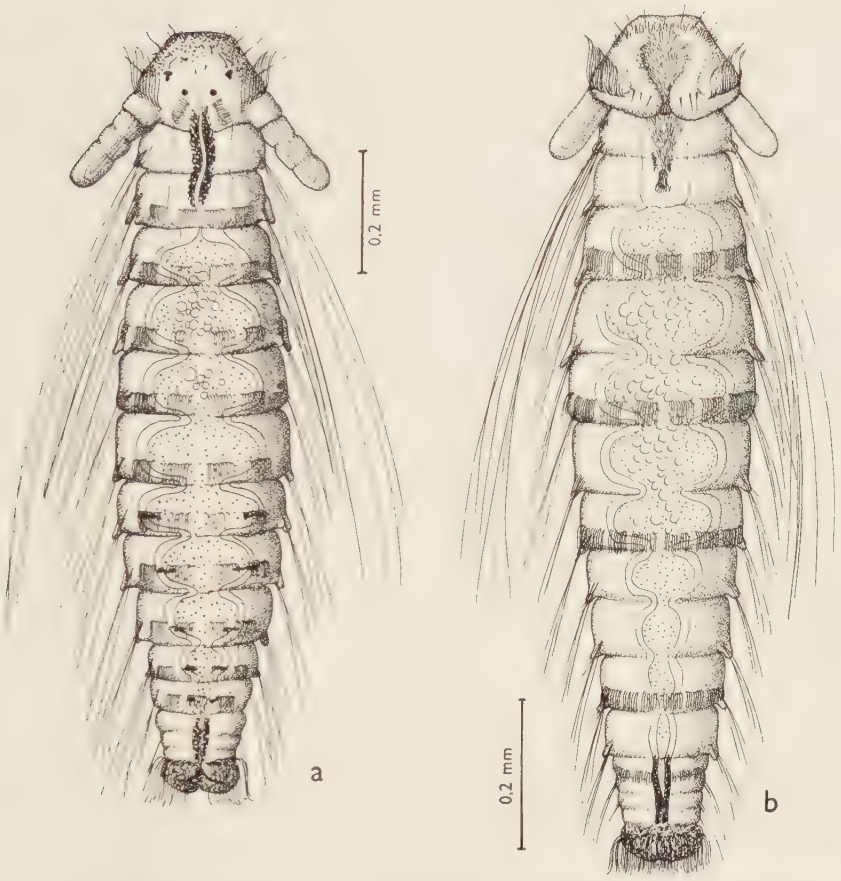


Fig. 43. *Polydora caulleryi* Mesnil. a) Big pelagic larva (dorsal view). b) Big pelagic larva (ventral view).

The young benthonic stage (fig. 44)

An individual with 20 segments and a length of 2.25 mm is described as typical of the stage.

The prostomium is somewhat notched and has acquired lateral rounded processes. In older stages it is further extended and develops a V-shaped notch at a tip. The eyes are unchanged (this was the case even one month after the metamorphosis). The nuchal crest has grown and become narrow (one month after the metamorphosis it had extended through segment 3). The palpi are very long (in older individuals they become as long as the entire animal). They are completely colourless. In all segments, i.e., even in segment 5, both dorsal and ventral cirri are found. They decrease posteriorly in length. Branchiae occur from segment 7 onwards. Nototrochs are still found from segment 2 onwards (they all are gradually reduced except

in the branchial region). The pygidium is stumpy and quadrilobate. It has retained its larval pigmentation and has acquired a number of "bacillary glands". The oesophagus is long and extends through segment 6. A rectum has been differentiated. In its most posterior part the black pigmentation is unaltered. Both dorsal and ventral hairy bristles are found in all segments. The modified bristles in segment 5 have acquired the specifically typical appearance. They are very robust (0.14 mm long and 0.015 mm thick). These distal parts are provided with a hood of fine fibrils, which has a darker colour than the remainder of the bristle (fig. 55b). These bristles are accompanied by six dorsal, "winged" hairy bristles which are relatively coarse, and nine ventral thinner capillary bristles of about the same length. From segment 7 onwards occur ventral crochets, three to four in each neuropodium. They do not exhibit any manubrial swelling and the distal serrations from a very small angle with each other. They are accompanied by relatively long, simple capillary bristles (fig. 44c).

Identity of species

The modified bristles and the ventral crochets are so characteristic of *Polydora caulleryi* that there can be no question regarding the identity of the species.

Biology

The metamorphosis is induced by pure sand as well as by shell fragments. In sand regular tubes are built of mineral grains and a secretion. Detritus and plankton are eagerly consumed.

Literature

Nothing was known earlier concerning the development in this species.

Polydora (Carazzia) antennata Claparède

In conformity with *Spio martinensis* (p. 75) two larval types occur here. These larvae develop however, in contrast to *Spio martinensis*, into benthonic stages, which although relatively similar can be distinguished from each other in all stages. In *Polydora antennata* Carazzi (1893) has described a variety, which he designated as "*pulchra*". This differs from the main species by not having its prostomium deeply notched, by an anal appendage which is not ventrally forked, and by palpi which are banded green and black. One of the larval types developes into the main species, and the other into this variety. The two larval types occur simultaneously in plankton (see p. 135). I never have found any intermediate forms among them. I therefore consider it appropriate to set up the first-mentioned variety as

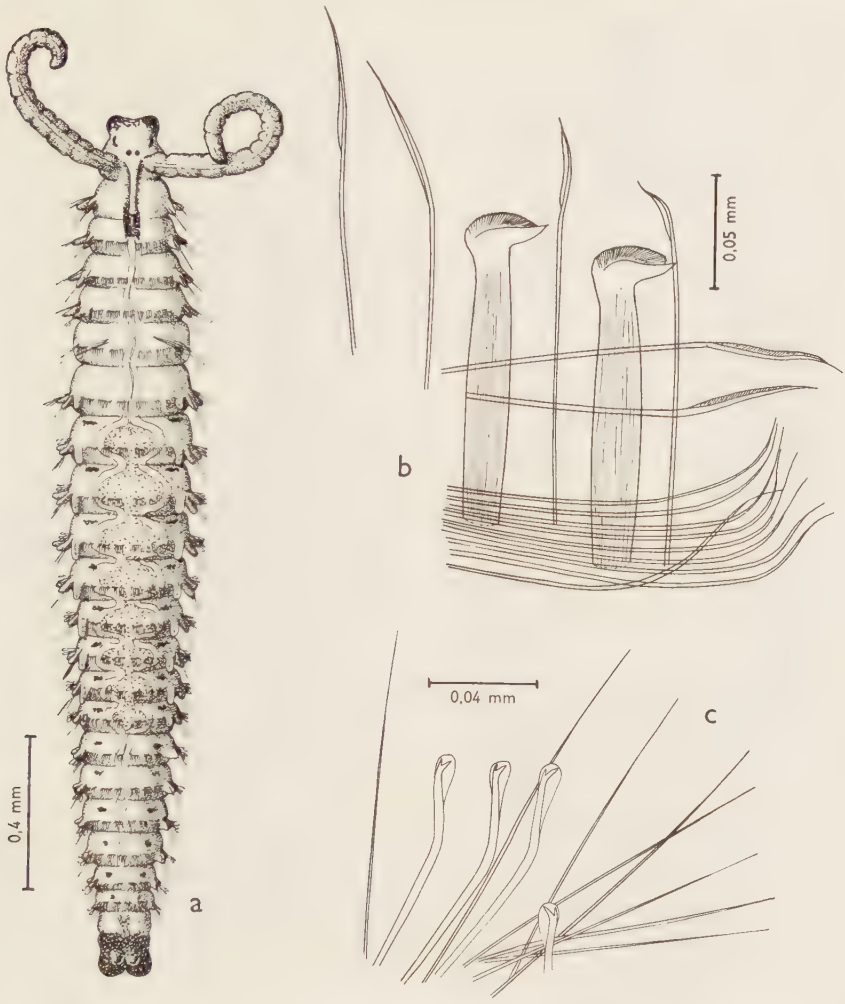


Fig. 44. *Polydora caulleryi* Mesnil. a) Young bottom stage (dorsal view). b) Bristles from segment 5 of the same. c) Ventral bristles from hind segment of the same.

a species with the name *Polydora* (*Carazzia*) *pulchra*. This species and *Polydora* (*Carazzia*) *antennata* must be regarded as closely connected.

Occurrence in the area of investigation

I have found this species on two occasions: once in the bay of Kristineberg at a depth of about 1 m in pure mineral sand (July 1951, no sexual products), and once in the sound between Kristineberg and Blåbergsholmen at about the same depth and the same kind of bottom (July 1952, no sexual products).

Occurrence in plankton

The larva occurs in plankton during the middle of the summer. It appears to be most abundant at the end of July, but occasional specimens have been encountered even as late as in October–November. The larva is always relatively scarce.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
11	0.76	0.22
13	0.86	0.26

With its short thick body this larva differs like the immediately following one from the usual *Polydora* type. It is distinguished from the larva of *Polydora pulchra* by its smaller size and fainter pigmentation. Green and yellow pigment are totally lacking.

The larva ready to metamorphose (figs. 45a, b)

Larval stages with 11 and 13–14 segments are chosen as typical specimens.

The prostomium is stumpy, somewhat notched terminally, and on the upper side provided with tactile cilia. The longest pair of these is attached anterior to the medial pair of eyes. The three pairs of black eyes are located in an approximately straight line when viewed from above. From this aspect the four median eyes appear round, and the lateral ones comma-shaped. Long tactile cilia are interspersed in the prototroch. The nuchal organs extend to the boundary between the peristomium and the first segment. On the nuchal crest there is a small occipital tentacle. Dorsal and ventral cirri are found in all segments. The dorsal cirri are more robust. Nototrochs occur from segment 3 onwards. The pygidium is rounded or provided with a dorsal and a ventral notch. The telotroch is well developed. The only dorsal pigmentation which is found consists of melanin. The prostomium lacks such pigment except in the eyes. In segment 1 there is a large median melanophore. In each segment from no. 4 onwards there is a pair of lateral melanophores, with branches towards the median line of the larva. A ramified melanophore is also found medially on the upper side of the pygidium. The oesophagus extends through segment 2. Behind it follows a brown-pigmented stomach, which about three segments from the pygidium merges into an unpigmented rectum. The larval setae be-

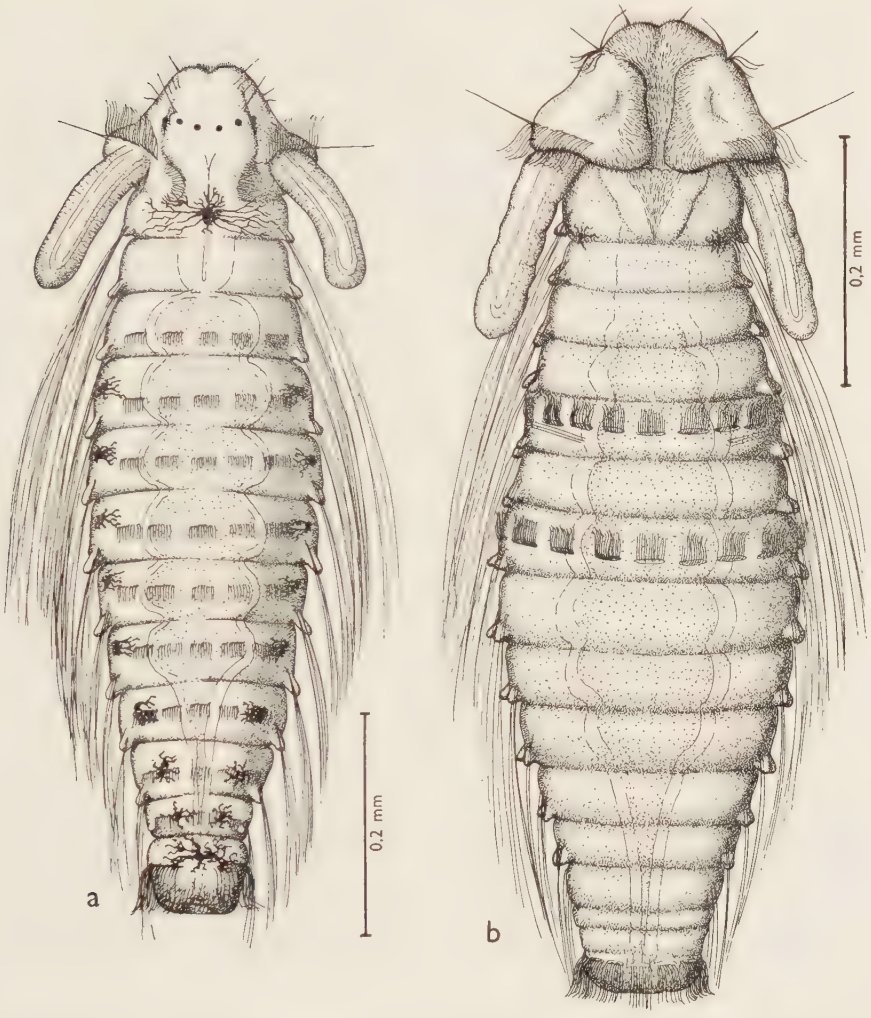


Fig. 45. *Polydora antennata* Claparède. a) Big pelagic larva (dorsal view). a) Big pelagic larva (ventral view).

come five to six segment lengths long and are almost non-iridescent in reflected light. In segment 5 there are already anlages to modified bristles of adult type. Ventral crochets are found from segment 8 onwards. Ventrally on the anterior side of the lateral lips there is a group of cilia, which may possibly be interpreted as an acrotroch. A "ciliated pit" is lacking. Gastrotrochs occur in segments 5, and 7. Ventral pigmentation is almost totally lacking. Between segments 1 and 2, however, a melanophore is observed.

The young benthonic stage (figs. 46a, b)

The description is based primarily upon one individual with 19 setigers and a length of 1.05 mm.

Towards the pygidium the body has a fairly evenly tapered shape. The "head" due the growth of the peristomium has become broader, but has also been elongated. Only two pairs of eyes are observed. The occipital tentacle has grown. The palpi have been considerably stretched, but are still entirely free from pigment. The nuchal organs extend posteriorly through segment 1. Well developed dorsal and ventral cirri are found in all segments except the fifth and the most posterior segments. In segment 1 the dorsal cirri are lifted higher up against the dorsal side than in the succeeding segments. Branchiae occur in segments 7, 8, and 9. Nototrochs are observed only in the branchial segments and in segment 6. They consist of single rows of ciliated cells (in older individuals I have observed double rows). The oesophagus extends through segment 6, where it merges into a stomach, which extends through segment 16. There it is followed by a convoluted rectum. The pygidium has a dorsal and a ventral notch. There are adult bristles in all segments both in the neuropodia and the notopodia except in segment 1 where notopodial bristles are missing. Ventral hooded crochets are developed from segment 8 onwards. The adult bristles are of the same type as those found in *Polydora pulchra* (fig. 48e–k), but are very much smaller and occur in smaller numbers.

Identity of species

By reason of the occipital tentacle, the characteristic modified bristles in segment 5, the appearance and occurrence of the ventral crochets, the lack of pigment on the palpi, and the ventral forking of the pygidium this larva must certainly be identified as *Polydora antennata*.

Biology

The metamorphosis is induced by mineral sand. The worm builds tubes which pierce the surface of the substratum perpendicularly, and rise relatively high above it. As constructional material it uses a secretion and its own fecal balls and, exceptionally, sand grains. It consumes detritus and plankton.

Literature

Thorson (1946, p. 96, fig. 48 A and B) has described two larval types, the identity of which he could not determine and which he combined under "*Spionid-larva B*" as he thought he had observed all transitions between them. The larger of these corresponds to the larva of *Polydora pulchra* (p. 131), and the smaller to that of *Polydora antennata*.

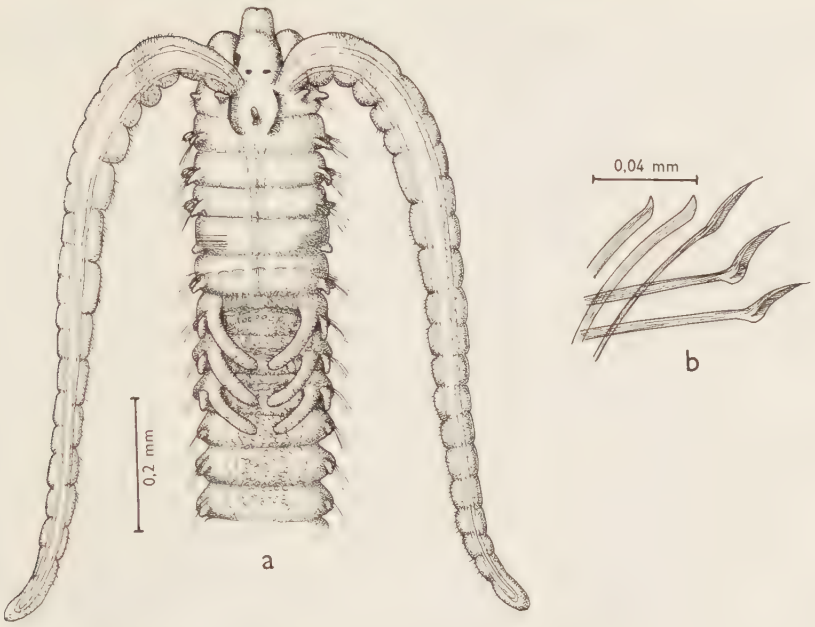


Fig. 46. *Polydora antennata* Claparède. Young bottom stage. a) Fore part (dorsal view). b) Bristles from segment 5.

Polydora (Carazzia) pulchra Carazzi

Occurrence in the area of investigation

I have found this species at a depth of about 10 m in mud, which smelled strongly of hydrogen sulphide, in the Trellebergskil north of Lysekil, and in sandy mud off Dalsvik in the Gullmar Fjord at a depth of 18 m. In the first case it was a large male with motile sperms (beginning of June), and in the latter two small individuals without sexual products (end of July).

Occurrence in plankton

The larva occurs in plankton from the end of May until the end of December. It can be very abundant at times.

Size and general characteristics of the pelagic larva

Segments	Length mm	Width mm
4	0.36	0.16
7	0.66	0.24
12	1.28	0.38
15	1.80	0.48
19	2.30	0.56

The larva differs from the foregoing primarily by its size and its more vivid pigmentation, where yellow and yellowish-green occur abundantly, and by its beautifully iridescent bristles.

The larva ready to metamorphose (figs. 47a, b)

Since this larva is earlier described (see p. 136) I shall not dwell upon a complete description, but shall only point out certain differences between it and the foregoing.

The lateral pairs of eyes coincide in dorsal view. The most lateral pair are not comma-shaped. The short palpi are usually pigmented yellowish-green and black (younger larvae may lack this pigmentation). The pygidium, which in the beginning is extended terminally, becomes at this stage rounded and acquires a dorsoterminal notch. The larva is richly pigmented. The melanophores are very large, ramified, and variable in form. This variability is dependent upon the intensity of the light. In larvae which have been kept for a few hours in a bowl with a white bottom the melanophores contract so strongly that at a first glance they appear as round spots. In individuals which have been kept in the dark the melanophores spread to such an extent that it can be impossible to distinguish their centres. Anterior to the lateral pair of eyes there is a pair of melanophores with branches in all directions, although chiefly cephalad. A large single melanophore is situated in the anlage to the occipital tentacle. Dorsally on the segmented part of the body there are four rows of ramified melanophores. The two median melanophores begin in segment 1 and are then found in all segments. The lateral rows begin first in segment 3. A single melanophore is situated on the pygidium. The prostomium has on the whole a diffuse yellowish-green pigmentation. There is a large yellowish-white (reflected light) chromatophore ventrally on the base of each palp. Chromatophores of this type are also found laterally in the middle part of the body (segments 6–8), and ventrally on the pygidium, where one or two may occur. The larval setae are relatively robust and strongly iridiscent in reflected light. Gastrotrochs appear irregularly. In different individuals they have been observed in segments 3, 5, and 9; in 5, 7, 11, and 13; in 5, 7, and 13; etc. The inside of the pharynx is pigmented reddish-brown or blackish-brown. Ventrally there are no melanophores, but the dorsal ones occasionally send down branches so that the ventral side can be strongly pigmented black fig. 47b).

The young bottom stage (figs. 48a–k)

One specimen which was examined one month after the metamorphosis had 33 segments and a length of 5.3 mm.

The "head" has become broader in relation to the rest of the body. The

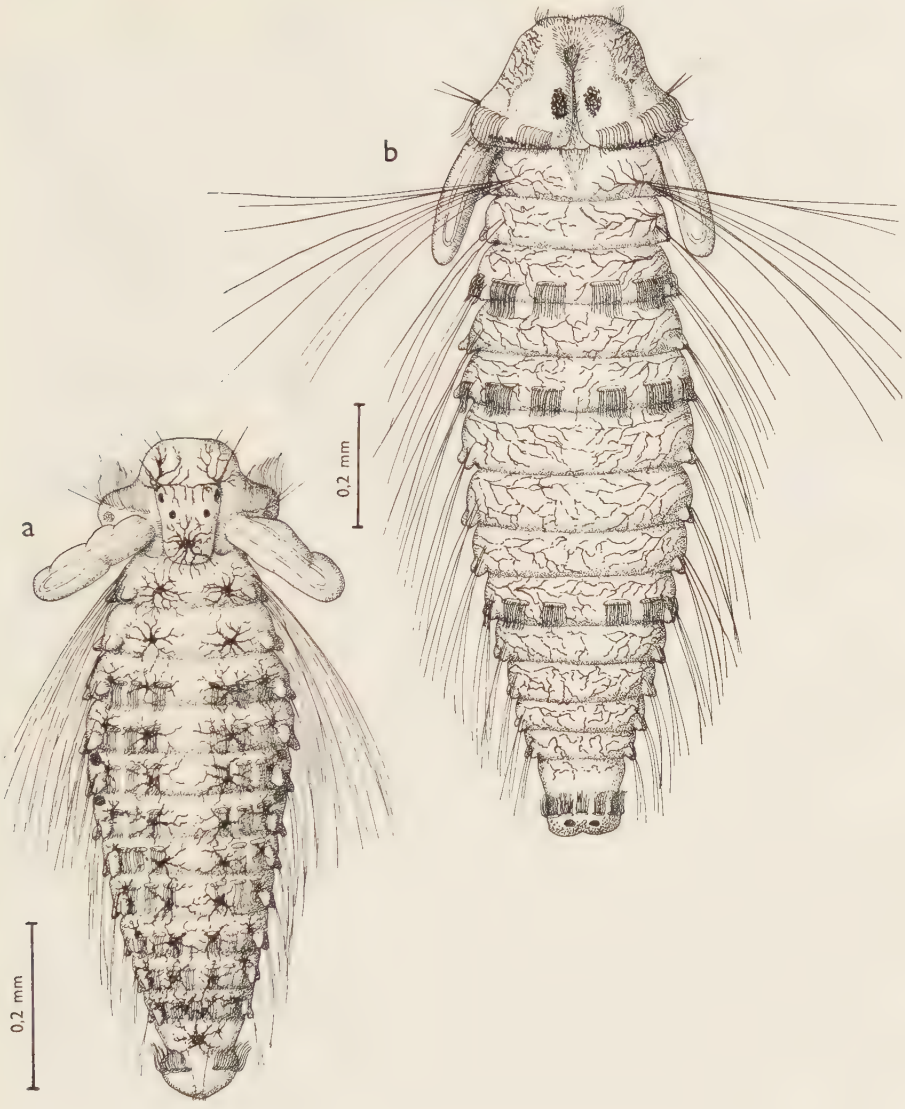


Fig. 47. *Polydora pulchra* Carazzi. a) Pelagic larva (dorsal view). b) Pelagic larva (ventral view).

prostomium has acquired a terminal notch and anlages to a pair of lateral processes (fig. 48a). The occipital tentacle has grown out. One pair of eyes has been reduced. The palpi have undergone an enormous extension so that they are now considerably longer than the entire body. They have become banded black and green transversally. The nuchal organs have developed into a pair of transverse grooves. The parapodia have acquired dorsal and ventral cirri except in segment 5. Branchiae are observed in

segments 7–12. In these segments, but not in any others, nototrochs are also found. The pygidium has developed into a typical "*Polydora* funnel" with a dorsal, but without ventral notch. The oesophagus extends through segment 10 and is colourless. The stomach, which is pigmented brown, extends through segment 24, where it merges into a convoluted but unpigmented rectum. Almost all the pigment has been reduced except on the palpi. The prostomium has a faint yellow pigment, and laterally in the segments of the middle part of the body the previously mentioned yellow chromatophores are still observed. The pygidium has a milkish opacity. In the vestibular tegmen a lobate ciliated structure has been differentiated. There are adult bristles in all segments both in the neuropodia and the notopodia, with exception of segment 1, where notopodial bristles are missing (figs. 48e k). Ventral hooded crochets are developed from segment 8 onwards.

Another specimen which was also examined one month after the metamorphosis (fig. 48c–d) had 41 segments and a length of 8.15 mm.

The dorsal cirri in segment 1 are in this stage carried higher up towards the median line of the worm. There are 13 pairs of branchiae beginning in segment 7. Ventrally in segments 6 and 7 is found a pair of very large glands with fibrous contents ("poches glanduleuses"; see p. 103). The pigmentation has undergone the most striking change. Prostomium, occipital tentacle, dorsal side of the peristomium, and dorsal side of segments 1–5 have become strongly pigmented black. The green pigment has about the same extension as in the foregoing stage. The adult bristles have increased in length. An individual which was examined two months after the metamorphosis had acquired 44 segments. It had sexual products from segment 13 onwards.

Identity of species

On account of the modified bristles in segment 5, the ventral crochets, the structure of the prostomium and the pygidium, and the vivid pigmentation I classify this larva as *P. pulchra* Carazzi (see p. 126).

Biology

The metamorphosis can take place as early as the 10–12-segment stage, but it can also be considerably postponed. Larvae with up to 23 segments have been obtained in plankton. The metamorphosis depends very slightly on the nature of the bottom substratum. The worm builds erect tubes, which extend far above the surface of the substratum. Plankton, detritus, etc. are ingested. The species is easily cultured. The pelagic larvae are at least partly predacious and capture other annelid larvae, even those which are larger than themselves, including individuals of their own species.

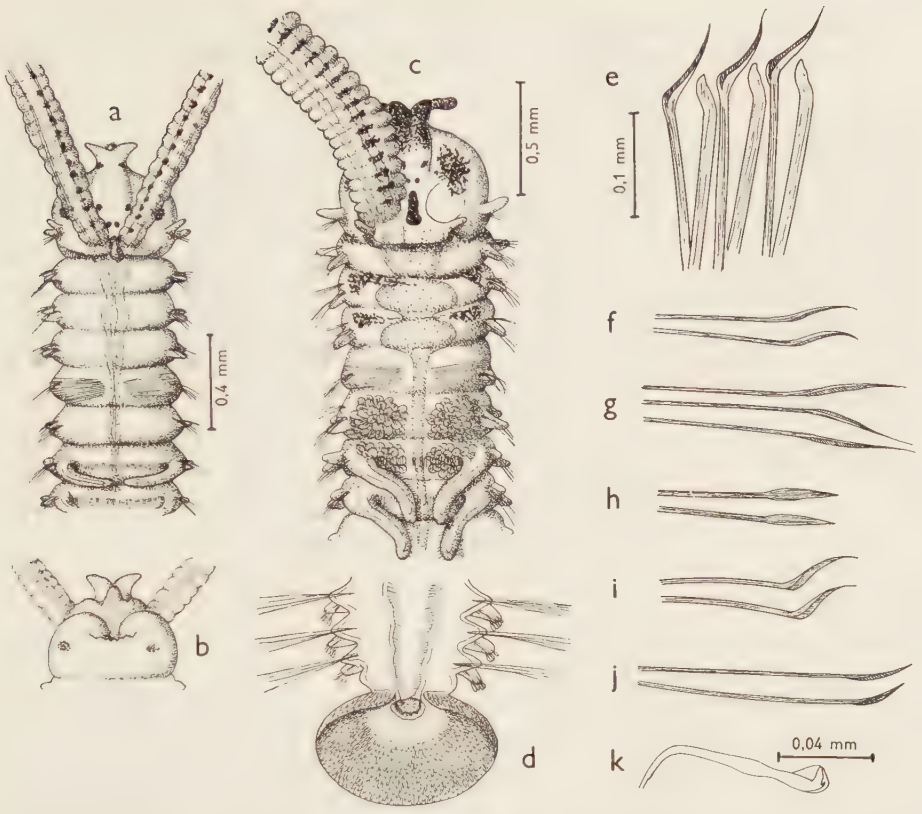


Fig. 48. *Polydora pulchra* Carazzi. a) Young bottom stage with 33 segments (dorsal view of the fore part). b) Ventral view of the "head" of the specimen in a. c) Young bottom stage with 41 segments. Right tentacular palp lost (dorsal view of the fore part). d) Dorsal view of the pygidium of the specimen in c. e) Modified bristles from segment 5 of the specimen in a. f) Ventral "winged" bristle from segment 1 of the same. g) Dorsal "winged" bristles from segment 5 of the same. h) Ventral bristles from segment 3 of the same. i) Dorsal "winged" bristle from segment 3 of the same. j) Dorsal "winged" bristles from segment 8 of the same. k) Ventral hooded crochet from segment 8 of the same.

Comparison between the larvae of P. antennata and P. pulchra

	P. antennata	*P. pulchra*
Occurrence in plankton	July until beginning of November.	May–December.
Eyes	The lateral ones appear comma-shaped when seen from above.	The lateral ones coincide with the next most lateral when seen from above.
Melanophores	Two dorsal rows.	Four dorsal rows.
Yellowish-green pigment	Lacking.	Abundant.
Size	Never more than 14–15 segments. Not over 1 mm.	Up to c. 23 segments. Reach more than 2 mm.

P. antennata is dependent on pure mineral sand for metamorphosis. The metamorphosis of *P. pulchra* is very little substratum specific.

Literature

The larva of *P. pulchra* has been well known for a long time. It was described for the first time by Claparède (1863) as belonging to *P. ciliata*. Several authors have shown that he erred regarding the identity of the species. The first who proposed that the larva should be referred to *P. antennata* was Mesnil (1896). One of the larval types which Thorson (1946) included under "*Spionid B*" should also be classified here (see p. 130). Finally, the larval development has been treated more completely by Casanova (1952).

B. *Poecilochaetidae* n. fam.

Poecilochaetus Claparède

The egg and sperm

The egg is discoid and has a thick egg-membrane and membrane vesicles. The sperm has a short head.

Type of development

The early development is not known but the type of the egg indicates that it is wholly planktonic. The pelagic larva is planktotrophic, and the pelagic stage is of very long duration.

The pelagic larva

The prostomium is rounded and there are two pairs of simple red eyes. Palpi are formed only very late. The lateral parts of the peristomium are small or lacking ("nectosoma stage"). The prototroch is first robust (up to the 30 35-segment stage), but is discarded later. The nuchal organs are first developed as a pair of longitudinal ciliated grooves on the sides of a nuchal crest. As this grows into a long, median occipital tentacle, the nuchal organs becomes very big. Nototrochs are lacking. The pigmentation is insignificant but yellow chromatophores (reflected light) are observed laterally from the second segment. The larval setae are short and thin, and are discarded during the later part of the pelagic life. A neurotroch and a "ciliated pit" are found. Complete gastrotrochs occur in all segments from the third onwards.

Key to species

1. Only one species, characterized as above. *Poecilochaetus serpens.*

Poecilochaetus serpens Allen

Occurrence in the area of investigation

In the area of investigation the species occurs in several localities, but always in pure mineral sand. It has been collected near the islands of Mittskär and Tova (G. Gustafson, verbal communication) and near the straits of Långegap (author's observations).

Occurrence in plankton

The larva occurs abundantly in plankton during July and August, and has been observed as late as in the middle of November (1952).

Size and general characteristics of the pelagic larva

Larvae of all stages from 7 segments up to 50 segments have been obtained.

Segments	Length mm	Width mm
7	0.54	0.18
50	8–10	

The larvae are very characteristic due to the nearly total absence of pigment. The larvae attract attention by their rapid serpentine manner of swimming.

The larval stages

The later part of pelagic life of the larvae can be divided into two stages.
I. Metatrochophora stage. In the metatrochophora stage the larva swims with the aid of well developed trochs. The larva has provisional setae, but no occipital tentacle. The larva remains in this stage until it acquires 30–35 segments.
II. Nectosoma stage. The trochs have been reduced. Locomotion takes place with the help of serpentine movement. An occiptal tentacle has developed.

The metatrochophora stage (figs. 49a–c)

The description is based on one larva with 7 segments, and another with 34.

The prostomium is broadened and richly ciliated. In its anterior part it is set with tactile cilia. Somewhat anterior to the eyes there is a pair of oblique ciliated bands, which laterally and ventrally pass into the ventral ciliation. In this structure the cilia do not appear to be bound to long ciliated cells of the kind found in the trochs. The lateral eyes are located

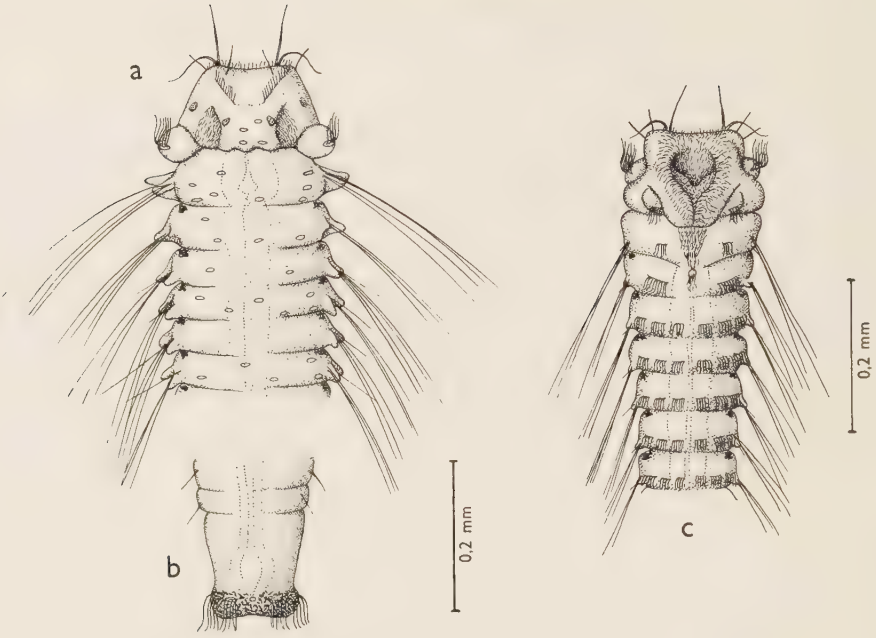


Fig. 49. *Poecilochaetus serpens* Allen. Young pelagic larvae (metatrochophora stage). a) Fore part (dorsal view). b) Hind part (dorsal view). c) Fore part (ventral view).

fairly ventrally. A broad and low nuchal crest is observed. On either side of this there lies a pair of richly ciliated nuchal organs. The occipital tentacle of the worm has not begun to develop. The peristomium is relatively weakly developed, but is of the same type as in the *Spionidae*. Dorsally it vanishes in a thin transversed integumental flap, which is attached at the posterior part of the nuchal crest, and which delimits the nuchal organs posteriorly. Palpi are still lacking in the 34-segment stage. In the 7-segment stage the anlages to the parapodial cirri can barely be discerned. In the 34-segment stage these have developed, but the segmentation is still homonomous in this respect. Nototrochs are lacking in all stages. The pygidium has the shape of a rounded knob, which is somewhat notched dorsally. The telotroch is very robust and dorsally discontinuous. The pigmentation is faint. From segment 2 onwards there occurs, however, in each segment a small yellowish-green (reflected light) chromatophore laterally on each side of every segment. It is lacking in the most posterior part of the body. Otherwise very small yellowish-green (reflected light) chromatophores are scattered in the epithelium. A pharynx is differentiated, but no other differentiations can be discerned in the alimentary canal. The lateral lips of the vestibule are weakly developed. In the vestibular tegmen an anteriorly directed small process is found. The slit-like aperture of the vestibule

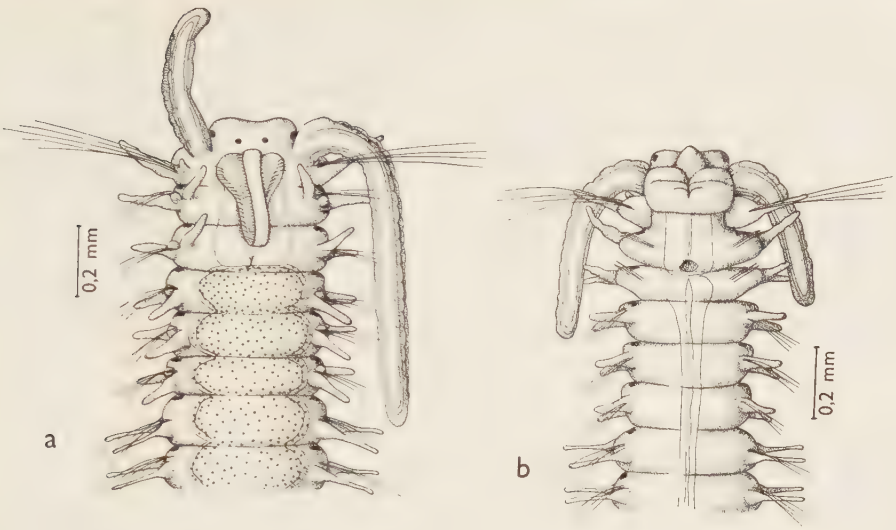


Fig. 50. *Poecilochaetus serpens* Allen. Old pelagic larvae (nectosoma stage). a) Fore part (dorsal view). b) Fore part (ventral view).

extends posteriorly through segment 1, which is thus partly divided medially. A very well developed "ciliated pit" is located in segment 2. The neurotroch is very broad in its anterior part. In segments 1 and 2 the gastrotrochs are represented by solitary lateral cells only. Behind they are, however, complete and consists of six ciliated cells each. There is no ventral pigmentation. In the youngest stages there are only thin larval setae; in the older individuals large adult bristles are found.

The nectosoma stage (figs. 50a–b)

The entire larval ciliation has now been discarded, and the larval setae have disappeared. A pair of palpi develop. One of them becomes somewhat longer than the other. The nuchal crest and the nuchal organs have now grown in their posterior end and together they have developed into the characteristic nuchal tentacle. It is laterally flattened and the nuchal organs on its two sides are set with fine cilia. Its proximal part is thickened to a heart-shaped portion the lateral parts of which represent anlages of two additional nuchal appendages. The lateral parts of the peristomium have now merged with the mouth region and can no longer be detected from the dorsal side. In the parapodia a very pronounced growth and differentiation has taken place. In segment 1 the ventral cirri have developed markedly, whereas the dorsal cirri are insignificant. In the five succeeding segments both the dorsal and ventral cirri are very robust and of about the same type. In segments 7–11 they are very long with a thicker proximal

portion and a distal swelling. The remaining segments have short, broad cirri both dorsally and ventrally. Of adult bristles there have appeared in segments 2 and 3 the specifically typical bristles which are coarse and somewhat curved at the tip. The pygidium has grown and acquired two pairs of cirri. The pigmentation is unchanged. In the alimentary canal the pharynx extends still more posteriorly. In the vestibule the previously mentioned process (p. 138) has developed further into a tapered, anteriorly directed, conical structure. The lateral lips of the vestibulum have been extended into the vestibule and are posteriorly distinctly separated from the first segment by the ventral lip. There is still a "ciliated pit" in the posterior part of segment 2.

Biology

The metamorphosis is induced by pure mineral sand.

Literature

This larva has been known since 1863, when Claparède described it as "*larva indéterminée*". Ehlers (1874) was able to determine its identity. McIntosh (1894) was evidently unacquainted with Ehlers' work, as he still treated the larva as "*Claparède's unknown larval Spio*". More recently the larva has been treated by Gravely (1909), Fauvel (1916), Flattely (1923), McIntosh (1927), and Thorson (1946). The egg has been described by Allen (1904) in his monograph on the species. He stressed the similarity with the egg of *Nerine cirratulus*.

C. *Disomidae* Mesnil

Disoma Oersted

The egg and sperm

The egg has a thick egg-membrane and membrane vesicles. The sperm has a short head.

Type of development

The early development is not known, but is probably entirely pelagic. The larva is predominantly planktotrophic.

The pelagic larva

The larva attains a length of about 1.25 mm. The prostomium and peristomium have coalesced into an outspread shield ("umbrella"). There are two pairs of red eyes. Palpi are formed relatively late. The prototroch is

robust and consists of two rows of ciliated cells. Nuchal organs and nototrochs are lacking. The pygidium is tapered in all stages; in older larvae it is provided with a pair of dorsal cirri. The telotroch is dorsally continuous. The larva is faintly pigmented. In young individuals larval setae are found in all segments, but they are gradually discarded except in segment 1. The "ciliated pit" is located in segment 2. In young larvae there are gastrotrochs in all segments from the third onwards, but they are later discarded.

Key to species

1. One species, characterized as above. *Disoma multisetosum.*

Disoma multisetosum Oersted

Occurrence in the area of investigation

In the area of investigation the species occurs in several localities. All localities lie at a depth of about 15 20 meters, and the bottom substratum is composed of black, foul-smelling, loose mud.

The species has been observed in the following localities: Trellebergskilen (G. Gustafson, verbal communication), Källeviken's ferry-bridge (G. Gustafson, verbal communication), and immediately south of the island Fredagsholmen in the Ellös Fjord (author's observations).

The egg and sperm (fig. 51a)

In the beginning of April 1952 two sexually mature males and one sexually mature female were obtained from Trellebergskilen. The eggs were discoid and had a diameter of 0.20-0.25 mm and a whitish colour. There were 30 32 membrane vesicles along the thin edge. The sperm had a length of 0.055 0.057 mm. The head was short and provided with a triserrated acrosome.

Occurrence in plankton

The pelagic larva occurs from the middle of March to the middle of May. It is most numerous in April, when at certain periods it can be the predominant species. Occasional specimens have been obtained as late as in July (1949).

Size of the pelagic larva

Segments	Length mm	"Umbrella" Width mm	Body Width mm
5	0.48	0.20	0.15
7	0.54	0.21	0.16
11	0.78	0.22	0.18
14	0.90	0.30	0.21
18	1.26	0.36	0.30

The 7-segment stage

The prostomium and peristomium are fused into an outspread "umbrella". There is a vestibule of the same type as in *Spionidae* and *Poecilochaetidae*, but in contrast to these families the lateral lips are here anteriorly fused. Posteriorly they forme a slit-like aperture (fig. 51c). Anlages of palpi are totally lacking. The prototroch is formed of two bands of ciliated cells, which follow the somewhat broadened edge of the umbrella. The first segment is more robust than the succeeding ones. None of the segments bear parapodia. Nototrochs are lacking. The pygidium is tapered terminally, pigmented brown, and bears a telotroch. In segment 1 there is a pharynx, which merges into a saccular "stomach", which in turn opens into a somewhat convoluted rectum in the last two or three segments. In addition to the pygidial pigmentation this larva has only small yellow pigment spots along the dorsal side. These pigment spots otherwise resemble those encountered in larvae of *Sabellaria* and *Poecilochaetus*. The larval setae in segment 1 are long and finely serrated. Adult bristles are lacking. A very special type of neurotroch is found. It is situated upon and on the sides of a low ridge in segment 1. In segment 2 there is a "ciliated pit", which consists of two contiguous divisions (fig. 51c). On either side of this there is a ciliated cell whose cilia swing in the longitudinal direction of the animal. In the succeeding segments there are two lateral ciliated cells, which represent incomplete gastrotrochs. They are somewhat obliquely directed in relation to the longitudinal axis of the animal.

The 11-segment stage (figs. 51b–c)

In this stage a pair of palpi has begun to grow. Their points of attachment are situated immediately posterior to the "umbrella". They are of different lengths. The first segment is no longer the most dominant as far as size is concerned. The body has its greatest width in segments 4–5. In the anterior segments parapodial cirri are under formation. The edges of the "umbrella" have acquired a reddish-brown pigmentation. The ciliated bands of the prototroch extend very clearly forward to the vestibule. In addition there is formed another ciliated band, which is located in the posterior part of the lateral lips. The ventral ciliation otherwise agrees with the foregoing stage.

The 18-segment stage

In this stage the palpi have further increased in growth. Otherwise the "head" has the same appearance as in the preceeding stage. The most noteworthy alteration which has taken place is the differentiation of the segmented part of the body. In segments 1 and 2 dorsal and ventral cirri have

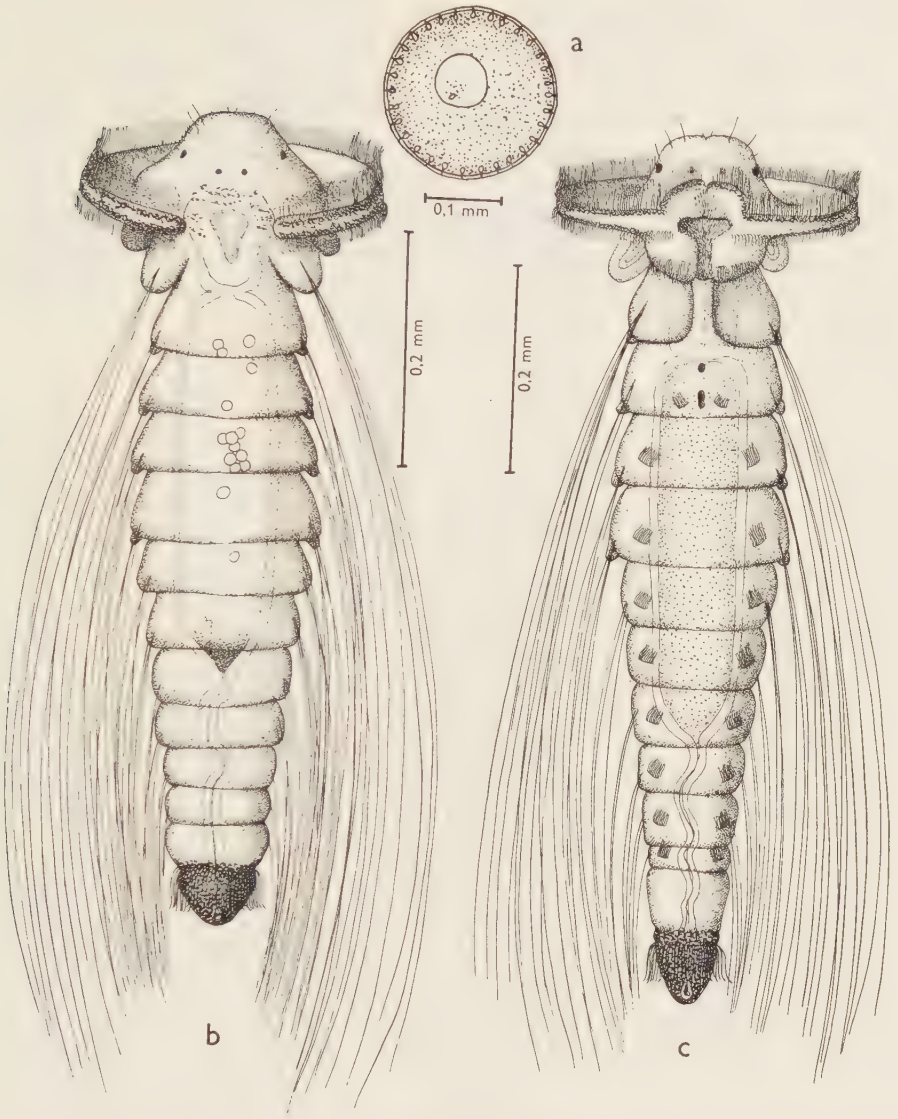


Fig. 51. *Disoma multisetosum* Oersted. a) Egg. b) Old pelagic larva (dorsal view). c) Old pelagic larva (ventral view).

grown to such an extent that they are considerably longer than in the succeeding segments, and have become somewhat anteriorly directed. In segment 3 where the cirri are smaller very strong bristles have developed (fig. 52b). Segments 4–8 have become very wide, and small dorsal and ventral cirri have been formed. In the following segments there is only one slender cirrus in each parapodium. Here relatively coarse, straight bristles

have been developed (cf. fig. 52c). Larval setae are still found in segment 1 whereas they have been discarded in the others. The neurotroch is still observed, but has a simpler appearance than in the foregoing stage, i.e., it consists only of a ciliated field in segment 1. The ciliation in the "ciliated pit" and the gastrotrochs have been discarded. On the pygidium a pair of anlages to cirri has appeared. The alimentary canal has been further differentiated and the oesophagus extends through segment 3. The stomach has acquired segmental diverticula. When the larva has attained this size, it swims folded into a doubled-up position. The folding is at the transition between the broader segments and those following.

The young benthonic stage (figs. 52a–d)

The description is based primarly on some specimens which were examined one month after the metamorphosis. The "head" has undergone great changes. The outspred "umbrella" has been reduced. The prostomium remains a heart-shaped, relatively small structure, which posteriorly terminates in a tip. On either side of this are the only rests of the "umbrella", a pair of small red pigmented callosities. The median pair of eyes is the only one which remains. The palpi have grown considerable, but are still of different lengths. (In all cases the right was longer than the left). On either side of the posterior part of the prostomium there is a pair of well developed nuchal organs. In the first segments the parapodial cirri have grown considerably, and are anteriorly directed. In segments 4–9, which here as in the big larvae are broader than the others, well-developed dorsal and ventral cirri are found. In the succeeding segments there is only one cirrus as in the big larva. The pygidium is now rounded and has acquired four cirri. Dorsal and ventral hairy bristles occur from segment 4 onwards. In segment 3, the coarse bristles have developed considerably (fig. 52b). There are two in each parapodium. In the following segments the hairy bristles are fairly thin and straight, and there are about six to eight per segment. In the succeeding segments are found bristles of another appearance. They are short and coarse, and the distal end terminates in a fine tip (fig. 52c). In segments 1 and 2 the alimentary canal has developed a robust and reversible pharynx. This is followed by a narrower part of the oesophagus which extends through segment 9. In segment 10 the gut is dilated, but is contracted again in the following segments. From segment 9 onwards there is a diffuse dark pigment.

Identity of species

The worm is so thoroughly characteristic that the identity of species must be considered established.

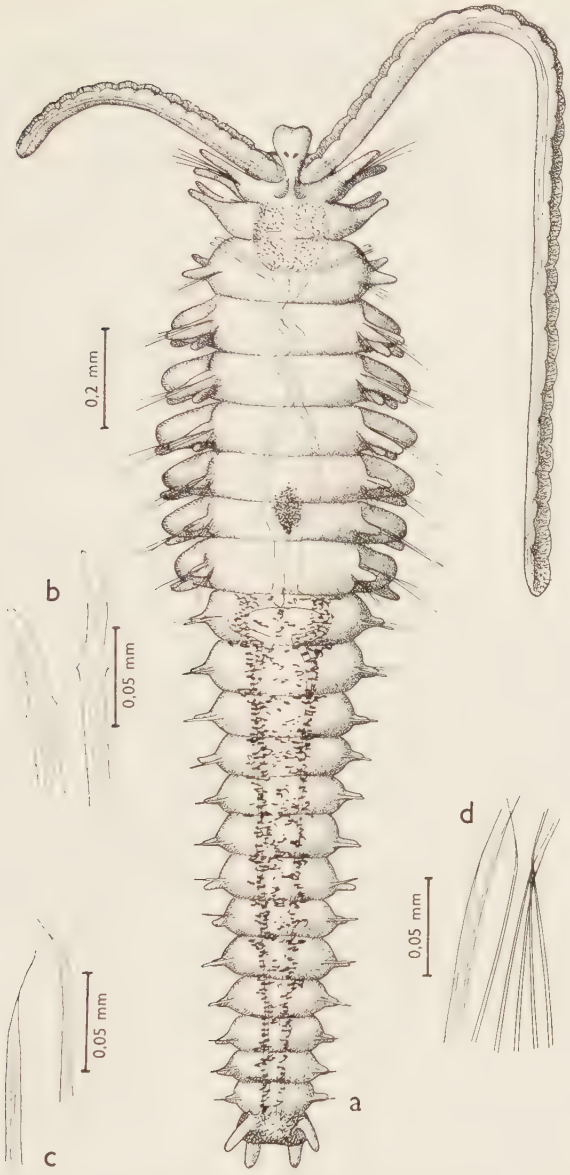


Fig. 52. *Disoma multisetosum* Oersted. a) Young bottom stage (dorsal view). b) Bristles from segment 3. c) Bristles from segment 14. d) Ventral bristles from segment 5.

Biology

It is difficult to get the larva to undergo metamorphosis in laboratory experiments. The recently metamorphosed worm builds tubes of mud particles and a secretion.

Literature

THORSON (1946, p. 102, fig. 55 A–B) insisted on classifying in this species a larva which, instead, should be referred to *Prionospio malmgreni* (cf. p. 46). The same author has, however, described a larva which he calls "*Spionid larva D*" which undoubtedly is identical with the one described here.

II. COMPARATIVE PART

Types of Development

With regard to the type of development three main groups can be distinguished within the families treated, viz. (I) species where the development is entirely pelagic, (II) species where the development takes place entirely or partially in structures produced by the female, and (III) species where the development takes place in the female body.

I. Development entirely pelagic

Claparède and Mecznikow (1869) demonstrated that *Nerine cirratulus* discharged its eggs directly in the water, and that the development was thus entirely pelagic, as Mesnil (1896) was later able to verify. Cunningham and Ramage (1888) found that the conditions in *Nerine foliosa* were the same. My own observations have revealed that these two species propagate in the same manner in the Gullmar Fjord. Complete pelagic development has not been demonstrable for *Nerinides tridentata*, but there is no reason to believe that this species should diverge from *Nerine* in this respect. In *Aonides oxycephala* so young planktonic stages have been found (p. 27) that it is quite probable that the development in this genus is also entirely pelagic. In *Laonice cirrata* I have been unable to determine whether it has an entirely pelagic development, but the egg type speaks in favour of this (see p. 25). This is also true of *Disoma* and *Poecilochaetus*. It is almost certain that the development is entirely pelagic also in *Spiophanes*. This is substantiated by my own observations of the early development in *Spiophanes kröyeri* and the finding of a young trochophore, which presumably belongs to this species (p. 37). Among the *Prionospio* species *Prionospio malmgreni* has been especially studied in this respect. Here it can be definitely established that the entire development is pelagic. A finding of a young larva probably belonging to *P. steenstrupi* indicates that this is also true of other species in this genus. Fage and Legendre (1927) obtained in nocturnal plankton sexually mature stages of *P. malmgreni* and *P. cirrifera*. This favours the view that spawning takes place in the pelagian, which is the case in many polychaetes, the best known belonging to the families *Nereidae* and *Eunicidae*, but also other families such as *Cirratulidae* (Caullery and Mesnil 1898, Gravier and Dantan 1928,

Stephenson 1950), *Scalibregmidae* (Fage and Legendre 1927, Gravier and Dantan 1928), *Ophelidae* (Fage and Legendre 1927), *Syllidae* (Herpin 1926), etc. In *Scolelepis fuliginosa* the eggs and sperms are discharged during a pseudocopulation (Claparède and Mecznikow 1869) when the sexually mature individuals wriggle together in a commonly secreted mucous mass. The subsequent development is wholly pelagic (Day 1934).

With regard to the conditions of nourishment of the larva the entirely pelagic development can be of two kinds. In the vast majority of species the amount of nutriment that the larva receives from the egg-yolk is sufficient only for carrying the development to the 2–3-segment stage. Thereafter the larva subsists on planktonic organisms. Here one can speak of a planctotrophic or perhaps more correctly of a predominantly planktotrophic type of development. In the *Aonides* species, however, the egg-yolk is sufficient for nourishing the larva until it is ready for metamorphosis. These larvae therefore do not ingest any food during their pelagic life. This type of development has been called lecithotrophic. The development in the lecithotrophic larvae seems to proceed much more rapidly than in the planktotrophic. I am under the impression that *Aonides* completes its planktonic life in ten to twelve days, whereas more than one month is required by *Prionospio malmgreni*, which has a planktotrophic type of development.

II. Development in structures produced by the female

A) Okuda (1946) described the jelly-like, stalked structure in which *Spio filicornis* embedded its eggs. These structures, which strongly resemble those encountered in *Scoloplos*, where attached to the bottom substratum by their narrower ends and were deserted by the females. In them the development took place until the larvae reached the 4-segment stage, whereupon the larva started on a planktonic life of long duration.

B) Structures of another type were first studied by Claparède and Mecznikow (1869) in *Microspio mecznikowianus*. They are composed of long, sling-like capsules in which the eggs are enclosed. Later capsules of this type have been observed in a large number of Spionids. They have been found in *Spio martinensis* (Mesnil 1896, Mesnil and Caullery 1917), *Pygospio elegans* (many authors), *Polydora quadrilobata* (Jakobi 1883), *Polydora polybranchia* (Mesnil 1896 and 1916), *Polydora ciliata* (many authors), *Polydora ligni* (Söderström 1920), *Polydora hoplura* (Wilson 1928), *Boccardia proboscidea* and *Polydora citrona* (Hartman 1941), *Polydora hermafroditica* (author's observations), etc.

The capsules is composed of a thin membrane, which surrounds the eggs. It may have the form of a long chambered tube (e.g. *Polydora ciliata*) or also consist of a row of separate divisions (e.g. *Polydora ligni*). Söder-

STRÖM (1920) advanced a theory of how these structures were produced. He believed that a secretion from the dorsally located vents of the epitoquous nephridia in the female was formed into capsules. These were then filled with eggs which escaped out from the vents of the nephridia. The capsules were thereafter closed and hardened in the water.

In the cases where these capsules are kept in the tube of the female one can speak of a primitive form of brood protection. Only one case is known where capsules of this type are deserted by the female, viz. in *Spio martinenis* (MESNIL 1896, MESNIL and CAULLERY 1917), where they lie floating in interstices in the substratum. In the majority of other species the capsules are attached to the wall of the female's tube. The female lies with the dorsal side towards her egg capsules and by movements of the cilia in the nototrochs produces a current through the tube and thereby secures a continuous oxygenation. In *Microspio mecznikowianus* the capsules are also kept in the female's tube, but in this species they are not attached to the wall but on the ventral side of the female (CLAPARÈDE and MECZNIKOW 1869). This observation has later been questioned by SÖDERSTRÖM (1920). In any case also this is a type of brood protection.

The duration of brood protection varies in different species. The majority has a short period of parental care and a subsequent long pelagic stage. As examples of this *Polydora ciliata* and *Spio martinenis Type I* may be mentioned. In these the larvae leave the capsule at the 3-segment stage and thereafter have a very prolonged pelagic stage. In *Polydora ciliata* this lasts at least four weeks. *Polydora hoplura* has a long period of brood protection followed by a short pelagic stage. In this species the larva does not leave the capsule before it has acquired about 17 segments. The pelagic stage then lasts only a day or a few hours (WILSON 1928). Presumably there are intermediate types between these two extremes. It is likely that *Spio martinensis Type II* has a relatively long period of parental care followed by a relatively long pelagic stage.

Spio filicornis is often mentioned as a species with varying duration of the brood protection. On page 66 this has, however, been shown to be a misconception. *Pygospio elegans* has, nevertheless, a period of brood protection which varies in length depending upon season. This species exhibits all transitions between a short brood protection and a subsequent, long pelagic stage in late winter, and a long brood protection with a very short pelagic stage in summer. Presumably the pelagic stage can be entirely eliminated (SÖDERSTRÖM 1920). The larva in all these cases are of one and the same morphologic type with the exception that the larvae which eliminate the pelagic stage entirely never develop larval setae (see further p. 97).

MESNIL and CAULLERY (1917) observed a peculiar manner of subsistence

among the larvae in one of the egg-capsule types, which they found to belong to *Spio martinensis*. These larvae consumed eggs and embryos in the capsule. They called this phenomenon adelphophagia. Later adelphopagia has been observed also in some other, Spionid species, viz., *Pygospio eleyans* (Söderström 1920), *Polydora hoplura* (Wilson 1928), and *Polydora hermaphroditica* (author's observations).

III. Development in the female body

A peculiar form of brood protection was found by Söderström (1920) in a species from the Falkland Islands, *Polydora natrix*. In this the epitoquos region of the female body with the fertilized eggs is constricted and forms a brood chamber for the larvae. The cuticle serves as a wall in this and the soft parts are disintegrated and consumed by the larvae together with unfertilized eggs. Söderström found in such a brood chamber larvae with 20 segments, which apparently had larval setae.

It is known that the developmental type in certain polychaete families is not bound to definite systematic groups, e.g. *Cirratulidae* (Gravier 1923), *Polynoidae* (Okuda 1946), *Eunicidae* (Gravier 1923, Krishnan 1936). In *Nereidae* species are even encountered where the developmental type varies, e.g. *Nereis dumerilii*. In this species there occurs in certain cases a brood protection with an inhibited pelagic stage, and in others an entirely pelagic larval development. In the families treated, the developmental type where the eggs are discharged into formed structures seems to occur exclusively in the four genera which Söderström (1920) united in the subfamily *Spioninae*, namely, *Spio*, *Microspio*, *Pygospio*, and *Polydora*. It has not been ascertainable in any case that the development of species belonging to these genera is entirely pelagic. On the other hand, it is exceedingly probable that all the other genera have an entirely pelagic development. It is also found that many adult characteristics which distinguishes the subfamily *Spioninae* from the other members of the family are just structures which may be interpreted as adaptions for their developmental type. The epitoquous nephridia are modified for the formation of spermatophores or egg-capsules, dorsal receptacula seminis are developed, etc.

Gravier (1923) thought that the majority of polychaetes discharged their sexual products directly into the surrounding water or onto the substratum without enclosing them in formed structures. An investigation on what is known of polychaetous development to date, shows that this is very probably not the case. The vast majority discharges its eggs instead into formed structures of different kinds, attaches them to the body of the mother, etc. As an example may be mentioned that out of 12 species of different genera which Okuda (1946) examined, 11 lay eggs in formed structures and only one has completely pelagic development. Regarding

the development of a large number of polychaetous species in Öresund THORSON (1946) wrote, "While all northern Echinoderms with pelagic larvae shed their eggs freely in the water this is only the case within a minority of the Polychaetes".

If it is postulated that all species belonging to subfamily *Spioninae* discharge their eggs into formed structures and that the others discharge them directly into the water, which is very likely, it is found that over 53 per cent of the treated species have a completely pelagic development, and with regard to the number of genera the corresponding figure reaches 69 per cent. These must probably be considered as relatively high figures in comparison with the rest of the order.

The Egg

With regard to the formation of the egg-membrane SÖDERSTRÖM (1920) could divide the *Spionidae* (in which family he also classified *Poecilochaetus* and *Disoma*) into two large groups, namely, those which had (I) eggs with thickened membranes, and (II) eggs without thickened membranes. The subfamily *Spioninae* was placed in the last-mentioned group and all the others in the first.

Eggs of the thick-membraned type in *Spionidae* were described for the first time by KEFERSTEIN (1862), who found them in *Colobranchus* (—*Scolelepis*) *ciliatus* and later they were reported by different investigators in a series of species belonging to *Spionidae*. GIARD (1881) assumed that this kind of eggs was characteristic of *Spionidae*. Later ALLEN (1904) found this egg type in *Poecilochaetus serpens* and I have found it in *Disoma multisetosum*.

Eggs of this type are usually somewhat flattened and have a circular or elliptical outline. The egg of *Aonides* constitutes an exception as it is spherical. The thick egg-membrane is perforated by a number of pores which lead into thin-walled vesicles.

The inner surface of the egg-membrane is smooth, but the outer is most often set with verrucose elevations (fig. 53e). These elevations give to the egg-membrane at lower magnifications in optical section a transversally striated appearance (fig. 53d). Frequently instead of verrucose elevations there is a system of ridges which run together in such a manner that the surface of the eggmembrane gets the appearance of a honeycomb (fig. 2a). This system of ridges is more conspicuous after fertilization. In *Spiophanes*, *Prionospio*, *Poecilochaetus*, and *Disoma* the elevations are relatively low.

The vesicles, which are connected with the surrounding water by means of the previously mentioned pores, have considerably thinner walls than the rest of the egg-membrane. They protrude into the plasm, which sur-

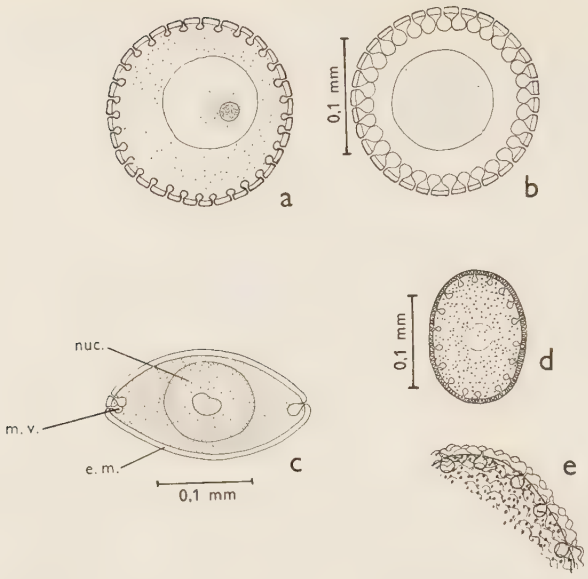


Fig. 53. a) A ripe egg of *Spiophanes kröyeri* Grube before fertilization, b) The same egg half an hour after fertilization, c) Cross section of an unfertilized egg of *Spiophanes kröyeri* Grube. nuc. = nucleus, m. v. = membrane vesicle, e. m. = egg membrane, d) An unfertilized egg of *Scolelepis ciliata* Keferstein, e) Detail of the same.

rounds them on all sides except at their small necks by which they are connected with the pores (fig. 53a–c). In the vast majority of species the pores are very fine. The *Aonides* egg constitutes an exception, here they are wide. In species which have discoid eggs the vesicles are usually found in one or two rows along the thin edge (figs. 53a, c) in others they may be more scattered. Upon the *Aonides* egg, which has one or two rings of such vesicles (fig. 7a) they are equatorially located. Here the plane of the circle is perpendicular to the longitudinal axis of the larva. This is not the case in those forms which have discoid eggs. There the longitudinal axis of the larva lies in the plane of the circle. In *Prionospio* there is a tendency towards reduction of the vesicles. In *P. malmgreni* they are totally lacking.

There has been a great deal of speculation concerning the function of the vesicles. Claparède (1864) believed that they were of significance in the formation of the blastoderm, and found that they contained a substance which was stainable with ammonia carmine. Cunningham and Ramage (1888) found in studies of the course of fertilization in *Nerine foliosa* that the membrane vesicles were destroyed thereby. They were of the opinion that the purpose of the vesicles was to reduce the specific weight of the egg. After fertilization the eggs should have the ability of floating freely in the water. Allen (1904) was of the opinion that in *Poeci-*

lochaetus serpens the vesicles secreted a substance to the surface of the egg.

In studies of the course of fertilization in *Spiophanes kröyeri* I have obtained another idea of the significance of the membrane vesicles. At fertilization there is a decrease in the volume of the plasm. It is possible to follow step by step how the plasm is released from the egg-membrane and the vesicles, and is concentrated towards the centre of the egg. Simultaneously with this process the vesicles increase in volume (figs. 53a–b). From this I have gained the impression that the vesicles are volume-regulation organs. The egg-membrane is namely so thick that it cannot follow the changes in volume of the plasm. The vesicles, on the other hand, have a thin and elastic wall. By the penetration of water from outside into the vesicles a constant hydrostatic pressure can be maintained within the egg-membrane. I have been unable to ascertain that the pores should serve as micropyles, as has been assumed by CUNNINGHAM and RAMAGE (op. cit.).

In a large number of cases it has been found that the egg-membrane in polychaete larvae has been converted into their first cuticle. There are, however, exceptions to this rule, e.g. *Spirorbis spirillum* and *Spirorbis japonicus* (OKUDA 1946), *Branchiomaldane vincenti* (MESNIL 1898), etc. It is not inconceivable that the same holds true for certain species belonging to the subfamily *Spioninae* (see p. 150). I have seen trochophores in egg-capsules of *Polydora ciliata* rotating inside their egg-membranes.

In other species belonging to *Spionidae* it is, however, possible step by step to follow the conversion of the egg-membrane into the larval cuticle. Good examples are provided by *Nerine foliosa* (figs. 2a–d) and *Aonides oxycephala* (figs. 7a–c). At first the egg-membrane surrounds the embryo and the young larva like an envelop. There is considerable space between the membrane and the larva. The membrane is, however, gradually filled out more and more by the growing larva. Its previously ridged or verrucous structure is smoothed out, and it becomes thinner, gradually lying close to the epidermis. Cilia and larval setae protrude from pores already at an early stage. I have found that the larval cuticle is formed in a similar manner in *Prionospio malmgreni* (figs. 12a–d) and *Spiophanes kröyeri* (fig. 10a), and it appears to be the rule for *Spionidae* with the exception of the subfamily *Spioninae*.

The thick-membraned type of egg discussed in the foregoing must be considered as unique in the polychaete system. There is a certain similarity in the eggs of the families *Euphrosynidae* and *Amphinomidae* (GUSTAFSON 1930 and verbal communication). They have, namely, a very thick egg-membrane with circular thinner parts, which thus might possibly be regarded as corresponding to the vesicles in *Spionidae*, *Disomidae*, and *Poecilochaetidae*.

In the closely related families *Ariciidae* (Eisig 1914), *Magelonidae* (McIntosh 1878), *Apistobranchidae* (author's observations), *Paraonidae* (author's observations), and *Chaetopteridae* (author's observations), on the other hand, the eggs have a thin egg-membrane and lack vesicles.

As previously mentioned this is also the case with the subfamily *Spioninae*. It seems likely that these eggs of Spioninae have resulted from a reduction of the thick-membraned type in connection with the change to brood protection.

The Sperm

Söderström (1920) found that the sperms of the *Spionidae* were of two types. The subfamily *Spioninae* had sperms with an extended head, while the others had sperms of the usual short-headed polychaete type. Furthermore, he was able to demonstrate that the extended form of the sperms in the subfamily *Spioninae* was due to the fact that these species developed spermatophores in the epitoquous nephridia of the males. In this family spermatophores were first observed in *Microspio mecznikowianus* by Köl-liker (1848). He thought that it was a question of gregarines, but Clapa-rède and Mecznikow (1869) were able to prove their true nature. Their morphology and manner of formation were described by the later authors, and subsequently by Cerruti (1908). Söderström (op. cit.) more recently found spermatophores in *Pygospio elegans*. These are of somewhat simpler type than those in *Microspio mecznikowianus*. Spermatophores occur in all genera belonging to the subfamily *Spioninae*. The development of spermatophores in this subfamily is connected with the phenomenon that these species lay eggs in formed structures. The egglaying is preceded by a copulation, in which the females receive sperm in the dorsal receptacula seminis (Söderström op. cit. and my own observations, see p. 115). On that occasion it must be advantageous to have the sperms collected in a spool-shaped spermatophore. The sperms proceed through the body of the female to the eggs where fertilization takes place (Söderström op. cit.).

External Morphology of the Larva

Prostomium

The prostomium is shaped first to an anteriorly rounded form which is differentiated in various ways. Prior to that stage certain genera have a tapered prostomium, as for example *Nerine* (figs. 2a b), *Aonides* (figs. 7 a–b), *Spiophanes* (fig. 10a), and *Scolelepis* (Day 1934), all of which have a thick egg-membrane. In the truncate stage the head region of *Nerine*

(figs. 2c–d) strongly resembles that of *Scolelepis* (figs. 16a–b). Later this similarity disappears more and more as a median process develops ventrally from the anterior part of the peristomium in *Nerine* (figs. 2d–e). In connection with the growth of this process there is also an anterior extension of the prostomium. It becomes terminally tapered and acquires on the under side a groove, which will partly enclose the peristomial process (fig. 2f). In *Disoma multisetosum* (figs. 51b–c) the prostomium forms together with parts of the peristomium a rounded shield or "umbrella" (cf. p. 142). The *Poecilochaetus* larva has a prostomium of the same type as the *Spionid* larvae.

In the pelagic larvae of *Nerine* and *Nerinides* (figs. 1–5) the prostomium is very slightly extended posteriorly. Similar but less pronounced conditions are found, e.g., in *Laonice* (fig. 6). In the others there is a tendency of the prostomium to extend posteriorly and to form a "nuchal crest" as the larva grows. A weak structure of this kind is found in the older larvae of *Spiophanes kröyeri* and *Prionospio*, but it becomes most strongly developed in the larvae of the subfamily *Spioninae*, the genus *Scolelepis*, and especially in *Poecilochaetus* where it develops into first one and later two additional tentacles. On the nuchal crest a small median occipital tentacle is developed in certain species (e.g. *Laonice cirrata*, *Polydora antennata*, *Polydora pulchra*, and *Polydora ligni*).

Eyes

As early as in the unsegmented trochophore one pair of eyes is formed. Later a number of eyes is often developed which exceeds that of the adult individual (e.g., subfam. *Spioninae* (see p. 150), g. *Scolelepis*, *Spiophanes kröyeri*, and *Disoma multisetosum*). The species treated may be divided into two large groups in regard to the number of eyes in the pelagic larva. One group comprises the genera *Nerine*, *Nerinides*, *Aonides*, *Laonice*, *Spiophanes*, *Prionospio*, *Poecilochaetus*, and *Disoma*, all of which develop two pairs of eyes. The other group comprises the subfam. *Spioninae* and the genus *Scolelepis* which develop three pairs of eyes. The larvae can be divided into the same groups according to the colour of the eyes. The first has red eyes (with one exception; *Prionospio malmgreni*), and the last mentioned black.

Häcker (1896) demonstrated that the eyes of Spionid larvae are composed of a central cell and a cup of pigment. The aperture of the pigment cup is variously directed in different pairs of eyes. In the subfamily *Spioninae* and in the genus *Scolelepis* there is one pair of eyes, the most lateral, which are compound. Eyes of this compound type have been described by Häcker (op. cit.) in his *Spio* larva ("Doppelaugenflecken"). Due to the fact that the pigment cup in the two parts of eyes of this type have variously

directed apertures, such double eyes when seen from above often appear kidney- or comma-shaped.

In conjunction with the metamorphosis there often occurs a reduction in the number of the eyes. This applies especially to the larvae which have three pairs of eyes. In these the next innermost pair disappears relatively soon. *Spiophanes kröyeri*, in which the adult lacks eyes, retains however, the larval eyes surprisingly long. I have found one specimen with 47 segments which still had them.

Peristomium

Posteriorly and ventrally the prostomium is delimited by the peristomium. Laterally and dorsally the peristomium is extended in a pair of sections which are more or less well demarcated from the rest of the peristomium, and from the prostomium. These I have called the lateral parts of the peristomium. Dorsally they may be connected by a low ridge, as is the case of *Nerine*, and *Nerinides*. In other species there is a tendency of this section to become overgrown (eventually displaced posteriorly) by the nuchal crest already in the larva (cf. p. 155). In *Nerine*, *Nerinides*, *Laonice*, *Scolelepis*, and *Aonides*, and to some extent in *Spiophanes*, the lateral parts of the peristomium are distinguished by being well developed and demarcated from the prostomium by a pronounced angle. In the others the lateral parts of the peristomium are less conspicuous and less well demarcated. The palpi are attached to the lateral parts of the peristomium. Frequently a palpophore is inserted between the peristomium and the palp. The palpophore may presumably be considered as a differentiation of the lateral part of the peristomium. In *Disoma multisetosum* special conditions exist (see p. 155). *Poecilochaetus* has small lateral parts of the same type as the *Spionidae*.

Ventrally the lateral parts of the peristomium pass into the longitudinal toric sections, which laterally limit the slit-like cavity known as the vestibule (Gravely 1909). These sections I have called the lateral lips. The vestibule is open anteriorly and ventrally. *Disoma multisetosum* constitutes an exception as here one section of the lateral lips has grown together anterior to the vestibule (fig. 51c). In the vestibular tegmen there are two pairs of pockets, one pair directed obliquely forward-upward-outward, and the other pair obliquely backward-upward-outward (cf. Salensky 1908). Medially there is a ridge (cf. Salensky 1908 "Medialfalte"). Of this ridge an anteriorly directed process is formed in certain species. Such a process is found, e.g., in *Polydora pulchra* (fig. 48b) and in *Poecilochaetus serpens* (fig. 50b). In the latter species Allen (1904) has called the process an unpaired tentacle. He regarded it as homologous to the lateral prostomial processes in *Scolelepis* which have fused into one. Thus it is instead a pro-

duct of the vestibular median ridge which is also found in *Scolelepis* where it is, however, not so well developed. This process has its most robust development in *Nerine* and *Nerinides*. In these it will affect the entire form of the "head" (see p. 12). It is supported by two longitudinal muscular bands (figs. 1b, 2d). In *Nerine foliosa* it is not developed until the larva has acquired two segments (fig. 2d). Posteriorly the vestibule is delimited ventrally by the anterior part of the first segment. This section has been called the ventral lip. The mouth opens into the posterior part of the vestibule.

The lateral lips and the vestibular tegmen are richly ciliated.

In conjunction with the metamorphosis the peristomium, like the prostomium, undergoes relatively marked alterations. This is especially noticeable in species where the lateral parts of the peristomium are well developed, and clearly demarcated from the prostomium. They become merged in the proximal parts of the palpi where for a time they can be detected as demarcated sections which strongly resembles the palpophores found in many spionid larvae. The ventral lip grows forward over the lateral ones, which thus will be drawn into the pharynx (see p. 186). The peristomium undergoes a very profound change in *Disoma multisetosum* in conjunction with the metamorphosis. The "umbrella" (p. 144) shrinks and persists for some time as a pair of insignificant pigmented callosities on either side of the peristomium. The similarities in the development of the "head" of *Disoma* and that of the archiannelid *Polygordius* are thus strong.

Palpi (tentacular palpi)

Palpi of varying length are developed during the pelagic life in almost all larvae belonging to the three families treated here. As a rule it may be said that in the subfamily *Spioninae* they are developed earlier than in the others. Especially in the genera *Nerine*, *Nerinides*, *Laonice*, and *Aonides* the palpi are developed late, and remain short during the pelagic stage. These genera together with *Scolelepis*, *Spiophanes*, and to some extent also *Prionospio* exhibit a characteristic property with regard to the points of attachment of the palpi. In these they are, namely, attached far out on the lateral parts of the peristomium. In others (e.g., subfam. *Spioninae*) they are attached closer to the dorsal median line.

Setigers, parapodia, and branchiae

As is the case in the archiannelid *Polygordius*, the segments are formed successively in the larva treated here. This is not so for example in the polychaete families *Polynoidae* and *Nereidae*, where a small number of primary segments are formed simultaneously, followed by the successive formation of further segments.

In the larva of the treated families, however, the two or three first segments have a special position in relation to the others. Here are found a neurotroch and a "ciliated pit", irregularities in the ciliation both dorsally and ventrally, etc. Segment 1 is always more robustly developed than the others, and acquires the longest larval setae. Segment 2, on the other hand, is often relatively weakly developed at first (see for example fig. 24a), even in relation to segment 3.

A number of segments is formed prior to the appearance of differentiated parapodia. This stage has been called by HÄCKER (1896) "Metatrochophora-stadium I", and the one with differentiated parapodia "Metatrochophora-stadium II". The differentiation occurs as a rule earlier in species belonging to g. *Scolelepis* and subfam. *Spioninae* than in the other.

Branchiae are formed in the larva above all in the subfamily *Spioninae*, but also in *Prionospio* and a *Nerine* species. In most of the species the first pair of branchiae are developed in the segment which definitely becomes the most anterior branchial segment. In some species, all belonging to the genera *Spio* and *Microspio*, this is not the case. In *Spio martinensis*, *Spio filicornis*, and *Spio multioculata* the branchiae are first developed in segment 2, whereas in the adult animal branchiae are found also in the first segment. In *Microspio atlantica* the first branchiae are formed in segment 3, and the adult animal has branchiae from segment 2 onwards. In these the most anterior pair of branchiae first develops late after metamorphosis. Branchiae are lacking in *Pygospio elegans* (which in the adult stage has branchiae from segments 11 12) during the entire pelagic life, and for quite a long time during the benthonic phase.

Larval ciliation

Two types of ciliation are found in the larvae: firstly a longer, connected with prolonged cells which are triangular in cross section, and, secondly, a shorter which is unattached to cells of this kind, and uniformly scattered over larger surfaces, for example, in the vestibule. Ciliation of the first-mentioned type is found in the proto-, noto-, gastro-, and telotrochs.

In addition there is a third type of cilia which cannot be classified in this system and which may be found interspersed among either of the foregoing types or occuring separately. These have been called "sensory cilia" by WILSON (1928), and occur most abundantly on the prostomium but also on the pygidium and the parapodia. When such cilia are found interspersed in the prototroch they are usually held outstreched from the body, but can also take part in the movements of the cilia of the prototroch. The isolated cilia of this type can also be observed in pendulation.

Trochs

PROTOTROCH

The course of the development of the prototroch has been specially studied in *Prionospio malmgreni*. The trochophore first developes a continuous, ciliated ring round the peristomium. Posterior to this a pair of lateral ciliated cells is then formed (figs. 12b d). The anterior ring is still unchanged in the 2-segment stage, but the posterior ciliated cells increase in size. Thereupon the anterior ciliated ring is completely reduced, but the lateral ciliated cells increase in number, and their cilia become longer. In *Nerinides* two consecutive rows of ciliated cells are found in the prototroch throughout the pelagic stage (fig. 1). It is conceivable that the anterior of these represents an incompletely reduced first row of cilia. In all the other Spionid larvae, however, only one row remains. In *Disoma multisetosum* the extremely robustly developed prototroch is composed of two rows during the whole pelagic life (figs. 51b d). *Poecilochaetus*, on the other hand, acquires an uniserial prototroch like the Spionids.

MESOTROCH

On the posterior part of the lateral lips a pair of large bundles of cilia are often found, which are separated from the prototroch (see e.g. fig. 51c). Presumably these represent rests of a posterior ring of cilia of the peristomium, the mesotroch, which is well developed in a series of larvae of other polychaete families.

NOTOTROCHS

As a general rule it may be said that the nototrochs develop earlier and more robustly in larvae belonging to the subfamily *Spioninae* than in the others. In some of these (not belonging to subfam. *Spioninae*) they are formed first after the metamorphosis. In the subfamily *Spioninae* complete nototrochs are formed in all segments except the first one or two, where they are, however, represented by occasional lateral ciliated cells. This is connected with the fact that the nuchal organs affect the formation of the nototrochs in these segments (see p. 167). Nototrochs are developed in the subfamily *Spioninae* usually at the 7 10-segment stage. In some species (*Spio martinensis* and *Microspio atlantica*) they are formed by two rows of ciliated cells. The first-formed becomes the posterior. These cilia lie posteriorly directed when at rest. The anterior row is weaker and is formed so that its ciliated cells alternate with those in the posterior row (fig. 27a). These cilia lie anteriorly directed when at rest. The nototrochs extend up on the side of the branchia which is directed towards the median line. In all other species belonging to the subfam. *Spioninae* the nototrochs are

never formed in the larva in more than one single row of ciliated cells per segment. *Nerine sp. II* has well-developed nototrochs, *Nerine foliosa* and *Nerine cirratulus* have weak ones, and in *Nerine sp. I* and *Nerinides* they are totally lacking. In *Spiophanes bombyx* well-developed nototrochs are found from segment 2, onwards but in *Spiophanes kröyeri* they are lacking in the anterior third of the body. In the *Prionospio* species they are developed late and only in those segments which later acquire branchiae. *Scolelepis* species have weak nototrochs; in *Laonice*, *Disoma*, and *Poecilochaetus* they are totally lacking in all stages. It is possible that this is also the case with *Aonides*. After the metamorphosis the nototrochs are lost in all segments except those which either do or will bear branchiae.

GASTROTROCHS

Gastrotrochs are found in all the species treated. In all cases they are composed of single rows of ciliated cells. They appear fully developed only from segments 2–3 onwards (in certain *Polydora* species and *Pygospio* still more posteriorly). This is connected with the fact that a neurotroch and a "ciliated pit" are formed. In the anterior segments isolated ventral ciliated cells, more or less obliquely placed, are found on either side of these structures. Presumably these should be regarded as incomplete gastrotrochs.

Gastrotrochs occur in all segments from no. 2–3 in *Nerine*, *Nerinides*, *Laonice*, *Aonides*, *Spiophanes*, *Prionospio*, *Disoma*, and *Poecilochaetus*, i.e. in all genera which do not belong to the subfamily *Spioninae* plus the genus *Scolelepis*. It should be noted that all these genera, in spite of great variations in shape and size of body, have the gastrotrochs arranged in essentially the same manner. Among these there are long slender forms (*Prionospio*), thick broad forms (*Nerine*), and very small forms (*Laonice*), etc. This indicates that the body form per se does not have any effect on the segmental occurrence of the gastrotrochs. The number of ciliated cells in the gastrotrochs varies greatly. In *Disoma multisetosum*, where the gastrotrochs are reduced in conjunction with the formation of a robust prototroch, there are only two ciliated cells per gastrotroch. Towards the end of the pelagic life these are also eliminated. *Spiophanes kröyeri* has also two ciliated cells per gastrotroch, but here the individual ciliated cells are extremely more robust than in the preceeding species. Otherwise they vary in number from four per segment (*Prionospio*) up to eight to ten in *Nerine* and *Nerinides*. Usually the gastrotrochs are most strongly developed in segment 3.

In *Scolelepis*, *Microspio* and *Spio* the gastrotrochs occur regularly in every other segment from no. 3 onwards and in *Pygospio* in segments 5 and 7. In *Polydora* they may occur according to the following schemes:

5, 7, 11, 13, and 15; 3, 5, 7, 10, and 12; 3, 5, 7, 10, and 13; 3, 5, 7, 9, and thereafter in all segments, etc. Like the prototroch and the telotroch the gastrotrochs are reduced in conjunction with the metamorphosis without leaving any trace.

TELOTROCH

The telotroch, i.e. the troch on the pygidium, often becomes very robust, even more so than the prototroch. This is the case, for example, in *Nerine* and *Scolelepis*. It is found in all the larvae examined, and is always built up by only one row of ciliated cells. In many species it forms a continuous band around the proximal part of the pygidium. In the majority, however, it is dorsally discontinuous. The formation of this dorsal gap is connected with the fact that the larval setae have such a length that they extend posteriorly outside the body. In these species the larval setae are held together in the dorsal gap.

"GRASPING CILIA"

In the larva of *Polydora ciliata* WILSON (1928) found small bundles of cilia laterally on the dorsal side of the setigers. These did not lash in the usual manner but made groping movements and were always curved. WILSON assumed that these cilia were for the purpose of holding together the larval setae, when they were laid along the back in swimming. In this manner they become more strongly attached to the back increasing thereby the stiffness of the larva. WILSON called these "grasping cilia". They are not so easily observable. They seem to be best developed in the subfamily *Spioninae* and the genus *Scolelepis*. Presumably they should be regarded as modifications in the nototrochs.

Intersegmental ciliation

On the anterior side of the parapodia a dorso-ventral row of ciliated cells is found in many larvae. This ciliation is for most part very difficult to observe. I have called it intersegmental ciliation.

Neurotroch and "ciliated pit"

Neurotroch is an established but unfortunate denomination of the ciliation which extends posteriorly from the region of the mouth along the ventral median line of the animal. It is a structure of an kind entirely different from the real trochs (se page 158).

In all larvae treated here the neurotroch is very short. It never extends farther back than segment 2. In its anterior part it is often broad, and passes without any boundary into the ciliation of the ventral lip. It narrows posteriorly and terminates with some exceptions in a little ciliated

cavity, in this work called "ciliated pit". This cavity was observed for the first time by GRAVELY (1909 A) in a few Spionid larvae, which he provisionally designated with the letters A and B. More recently DAY (1934) found such a structure in the *Scolelepis fuliginosa* larva and described it, apparently without being acquainted with GRAVELY's paper.

This organ is found in all the examinated larvae with the exception of *Pygospio* and the majority belonging to *Polydora*. In *Aonides* it has not been possible to decide whether there exists a "ciliated pit" or not. In all other families than those treated here it is, however, lacking. I have examined numerous larvae of the families *Magelonidae*, *Nereide*, *Nephthydidae*, *Polynoidae*, *Eunicidae*, *Phyllodocidae*, *Sabellaridae*, *Serpulidae*, *Amphictenidae*, etc. without finding any analogous structure. The "ciliated pit" appears thus to be exclusively characteristic of the families *Spionidae*, *Disomidae*, and *Poecilochaetidae*. I consider this of great importance from a systematic point of view (see p. 175).

The "ciliated pit" is located in segment 1, 2, or 3, and may have a variable form. Usually it is a more or less slit- or keyhole-shaped, but at times rounded cavity. In *Disoma* there are two successive cavities. A common property of all them, however, is that the posterior part of the "ciliated pit" is provided with a number of fairly robust cilia directed towards the bottom of the cavity, and the anterior part with shorter cilia likewise directed down towards the cavity. At the transition to the neurotroch there is frequently a number of stiff cilia which are transversally directed. These often performe slower pendulous movements. In *Prionospio steenstrupi* there are two areas with complicated ciliation behind the "ciliated pit" (fig. 14c). This species diverges by this property from all the others.

In larvae belonging to the genera *Nerine*, *Laonice*, and *Scolelepis* a pair of finely ciliated swellings are sometimes observered on either side of the neurotroch (fig. 6c). Similar structure have been observed also in the young *Polydora ciliata* larva by WILSON (1928). These are lost like the rest of the neurotroch "ciliated pit" complex in conjunction with the metamorphosis or even earlier.

On studying preparations of larvae stained with iodine green it is found that the "ciliated pit" is the common vent for two systems of mucous glands. These glandular systems are most markedly developed in *Scolelepis*, *Spiophanes*, and *Spio* (figs. 54b, d, e.). In these the "ciliated pit" is actually a double structure. In the posterior part, where it forms a rounded cavity, unicellular glands open; in the slit-shaped anterior part a short, median, anteriorly directed passage opens which terminates blindly anteriorly. Four gland-like epithelial tubes open on either side in this passage. The first pair is anteriorly directed. The distal parts are thickened like those in the following tubes, and located in the anterior part of segment 1. The

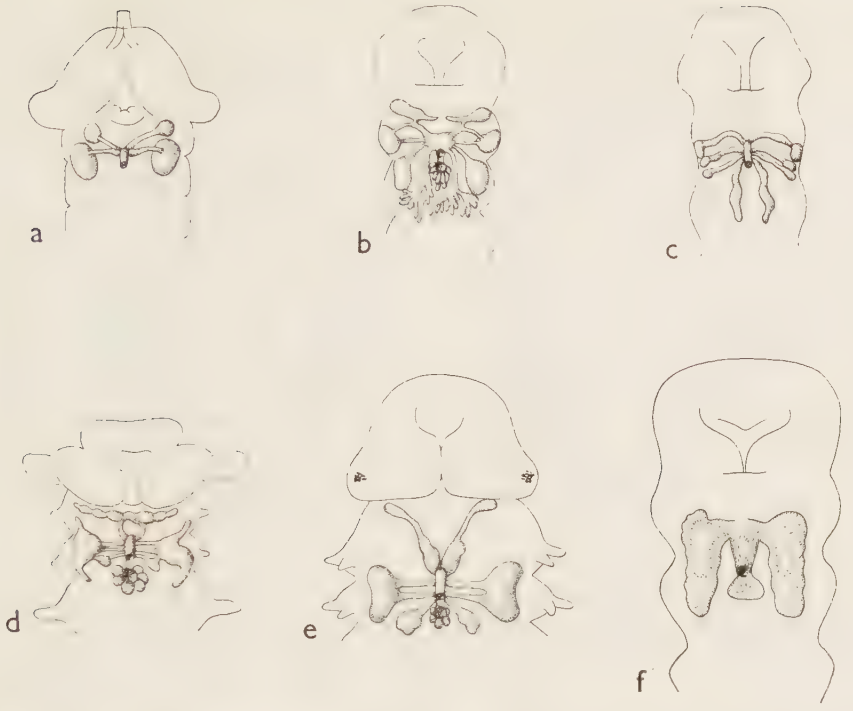


Fig. 54. Ventral views of the fore parts of larvae stained with iodine green showing the ciliated pit complexes. The body walls are only roughly sketched. a) *Nerine foliosa* (9-segment larva). b) *Spiophanes kröyeri* (14-segment larva.) c) *Prionospio steenstrupi* (12-segment larva). d) *Scolelepis fuliginosa* (9-segment larva). e) *Spio martinensis* (17-segment larva). f) *Poecilochaetus serpens* (36-segment larva).

second and third pairs of the tubes lie closely together and are the most robustly developed. The distal parts are markedly thickened, laterally situated, and in *Spio* and *Scolelepis* fused. In *Spiophanes* the conditions are somewhat different. Here the distal parts are not fused, and are laterodorsally situated. There is an anastomosis between the first and second glandular tubes on either side. The last pair of glands is posteriorly directed. These glands are small in *Scolelepis*, but very large in *Spiophanes*. In *Prionospio*, *Nerine*, *Nerinides*, *Poecilochaetus*, and *Laonice* (figs. 54a, c, f) the posterior part is lacking. In the first-mentioned genus the four pairs of glandular tubes are weakly developed. This applies also to *Laonice* where the glandular tubes are relatively short. In *Nerine* and *Nerinides* the number of glandular tubes is reduced to two pairs. This is also the case in *Poecilochaetus* (fig. 54f) where they are, moreover, very robust and located under each other. The median ciliated passage in this genus is very robust and easily observable in balsam preparations of whole specimens. *Disoma*

seems to possess no glands in connection with the two cavities (see the foregoing). At least I have not succeeded to stain them with iodine green.

Fig. 55a shows a cross section through the "ciliated pit" region immediately anterior to the vent in the larva of *Nerine cirratulus*. The median ciliated duct (m.c.d) is discerned medially in the ventral side, immediately under the epithelium. On the one side it is seen how the glandular tube runs ventrally around the connectivum in the ventral nerv cord (v.n.c.). From here it then curves into the coelom, pushing the somatopleura before it. On the other side of the oesophagus (oes.) the gland is bisected, but the section has not hit the downward passage. The cells which form the gland are very large and provided with big nuclei rich in chromatin. The nucleoli are strongly refractive and large. The glandular contents which on fixation coagulate to a homogeneous mass with fine cracks are stained blue with azan. The cells which surround the proximal part of the glandular lumen are of another type than the distal ones. They are appreciably smaller and have smaller nuclei. Figure 55b shows in a somewhat more posterior section how the median ciliated duct opens into the "ciliated pit" (c.p.).

The formation of the "ciliated pit" has been studied in *Prionospio malmgreni*. Traces of this organ complex are first seen relatively late in the 2-segment stage (fig. 12d). It appears at the place where the prolonged blastopore had its posterior part before it began to close. It is, however, no direct rest of the blastopore, as this has become completely closed before the "ciliated pit" is first observed. The glandular complex grows after that, and attains its fullest development immediately before the larva is ready to metamorphose.

The "ciliated pit" complex is wholly a larval organ. Already six hours after the metamorphosis it is strongly reduced in *Spio martinensis*, and after 16 days no trace of it is left (fig. 58b–c). Staining with iodine green of such recently metamorphosed worms reveals that also the glands have been reduced.

In view of the position immediately adjacent to the ventral nerv cord Day (1934) thought that the "ciliated pit" had some sensory function. This author had not observed the glandular nature of the organ. That it is actually a question of a glandular complex which produces mucus is shown by the intensive staining with the specific mucus-stain iodine green, and by the blue tone when stained with azan. It is conceivable that the gland produced mucus for the first tube, when the larva passes over into a benthonic life.

It is interesting to note that the "ciliated pit" is lacking in the larvae which must be considered the least primitive, viz. *Polydora* (with one exception) and *Pygospio*. In the bay of Kristineberg species with larvae provided with a well developed "ciliated pit" occur in the same locality as

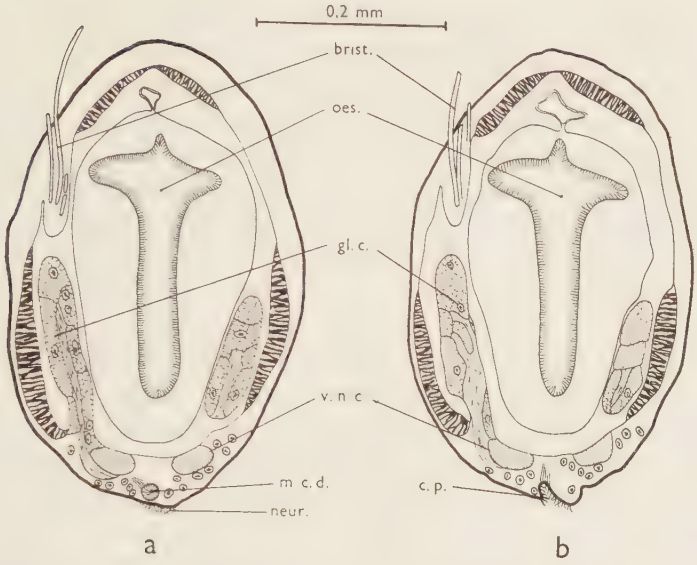


Fig. 55. Cross sections through segm. 2 of a big pelagic *Nerine cirratulus*-larva showing the ciliated pit complex. a) Immediately anterior to the ciliated pit. b) Through the ciliated pit. brist. = bristles, c. p. = ciliated pit, gl. c. = gland cells, m. c. d. = median ciliated duct, neur. = neurotroch, oes. = oesophagus, v. n. c. = ventral nerve cord.

Pygospio elegans and certain *Polydora* species. They have similar modes of life, and build similar tubes. It seems thus as if a "ciliated pit" had very little biological significance for the larva. Instead the "ciliated pit" complex should probably be regarded as a palingenetic organ which is reduced in the most advanced species.

The "ciliated pit" complex shows many similarities to the foot glands of the prosobranchs and some pulmonates. According to Lang (1888) the foot glands of these gastropodes are of two kinds. He characterized them as follows:

"1) Die unpaare vordere Fussdrüse mündet bei den Prosobranchiern am Vorderrande des Fusses und zwar bei denjenigen Formen, bei denen dieser Vorderrand in einen oberen und einen unteren Lippensaum gespalten ist, zwischen den beiden Lippen (Lippendrüse). Bei den Pulmonaten öffnet sie sich zwischen Kopf und Fuss nach aussen. Sie stellt einen verschieden langen, nicht selten die Länge des Fusses erreichenden Epithelschlauch dar, welcher meist in die Fussbasis eingeschlossen, seltener ihr in der Leibeshöhle aufliegend, von ihrer Mündungsstelle median nach hinten zieht. In die Wandung des Schlauches, welcher als Reservoir und Ausführgang dient, münden zahlreiche einzellige Schleimdrüsen, die im umgebenden Fussgewebe liegen. Die Drüse sondert Schleim ab. Mit Unrecht ist sie als Geruchsorgan bezeichnet worden. Sie unterliegt, was ihre Grösse, die Gestalt

ihres Querschnittes und was die Zahl, sowie Anordnung der Drüsenzellen anbetrifft, bedeutenden Modificationen.

2) Die unpaare Fussohlendrüse ist bei den Prosobranchiern weit verbreitet. Ihre äussere spaltförmige Öffnung liegt hinter dem Vorderrand des Fusses in der Mittellinie der Sohle und führt in eine als Reservoir fungierende im Fusse gelegene Höhle, deren Epithelwand in das Lumen entspringende Falten bildet. Die Höhle ist allseitig von einzelligen Drüsen umgelagert, welche ihr Secret vermittelst ihrer zwischen den Epithelzellen mündenden Ausführgänge in sie entleeren. Mit recht ist diese Fussohlendrüse der Prosobranchier als ein der Byssusdrüse der Lamellibranchier homologes Organ betrachtet worden. Ihr Ausbildungsgrad ist sehr verschieden und nicht selten fehlt sie ganz."

In many of the larvae treated here, as in many of the prosobranchs, there are thus two ventral unpaired mucous gland complexes which show great similarities. The unpaired anterior foot-gland should correspond to the anterior of the "ciliated pit" glands, i.e. that which have a median ciliated duct, and the unpaired foot-sole gland to the posterior part. In this connection it shall be pointed out that there are two different depressions in the "ciliated pit" complex of *Disoma multisetosum* (p. 142). There are, however, some dissimilarities. In the prosobranchs the anterior unpaired foot gland is unbranched and posteriorly directed, in the Spionid larvae, however, the anterior "ciliated pit" gland is branched and anteriorly directed; the cavity of the posterior unpaired foot-sole gland is in the prosobranchs often provided with folds, but in the larvae treated here, the wall of the posterior cavity is, when existing, smooth. Regarding these dissimilarities one must remember that the comparison has been made between larvae, on one hand, and adult animals, on the other. Unfortunately the larval development of the foot glands in the prosobranchs seems to be very little known. Moreover, it must be supposed that the foot glands of the prosobranchs, which have a biological significance, have developed a series of modifications which distinguish them from those of their ancestors. In the larvae treated here, in return, the glands seem to have very little biological significance, and are exclusively larval organs.

Furthermore the finely ciliated swellings on either side of the posterior part of the neurotroch, which are lost in conjunction with the metamorphosis (p. 162), show certain similarities to the first anlage of the foot in the prosobranchs. In *Patella* (Patten 1886), for instance, the footanlage is first observed as a pair of lateral swellings on either side of the slit-shaped blastopore, which is closing from behind and in front. Later on these swellings will fuse and give rise to the foot.

In my opinion these similarities indicate that the "ciliated pit" complex and the ciliated swellings of the larvae treated here, on one hand, and the

foot glands and the foot of the prosobranchs and (to a certain extent) the pulmonates, on the other, could be regarded as homologous organ complexes.

This in turn naturally presupposes a common ancestor of the polychaetes and the gastropodes. As the families treated here are the only among the *Polychaeta* which have this organ complex, they must be placed in a central position in a genealogy of this order. The conception of the Spionids as primitive polychaetes has, for other reasons, been advanced earlier by Mesnil (1925) and others.

Nuchal and dorsal organs

Gravely (1909) found structures in the "neck region" of the Spionid larvae which he called "ciliated grooves". He did not make any attempt to interpret their nature. The same is true of Wilson (1928), who discovered a fine, rapidly moving ciliation on either side of posterodorsal part of the prostomium in the larva of *Polydora ciliata*. Day (1934) found no such organs in the larva of *Scolelepis fuliginosa*.

Nuchal organs occur in almost all of the examined larvae. The only larvae where I have not found them are those of *Laonice* and *Disoma*. The former in the adult stage has very long, parallel nuchal organs, and the latter almond-shaped ones. In all the others a pair of ciliated grooves is formed, which develop in various ways. They are usually formed early. Transversally placed groove-shaped nuchal organs on the anterior part of the peristomium ahead of the prototroch characterize the larvae of *Nerine* and *Nerinides*. Those of the *Spiophanes bombyx* and *Aonides* larvae are of the same type, but here they originate in the posterior part of the peristomium behind the prototroch. In *Spiophanes kröyeri* they are longitudinal. In the young *Poecilochaetus* larvae and in the *Prionospio* larvae the nuchal organs are more or less almond-shaped or oval. In the nectosoma stage of *Poecilochaetus* (p. 139) the nuchal organs together with the nuchal crest undergo an enormous development so that they finally form a tritentacular ciliated structure. In all species belonging to the subfamily *Spioninae* the nuchal organs originate as a pair of more or less parallel grooves on either side of the nuchal crest. Both the nuchal crest and the nuchal organs increase posteriorly. During growth, the nuchal organs develop in different manners in different species. In *Pygospio elegans* they do not extend appreciably in a posterior direction, but are only broadened and become a pair of obliquely placed oval structures. In the *Polydora* species, on the other hand, they continue to grow parallelly and in different species reach varying lengths. *Polydora pulchra* constitutes an exception; here they finally forme a transverse groove in the first setiger. In the *Spio* and *Microspio* species the growth after metamorphosis results in separation of the nuchal organs in

the first segment, which were parallel at first, and in their re-approximation in the third (see for example figs. 24b and 25a). In this manner they will surround the middle portion of the second segment like a horseshoe. In the *Scolelepis* species the growth of the nuchal organs takes place in a similar way.

Metameric dorsal organs are very rare in the pelagic larvae, but are formed occasionally very soon after the metamorphosis. In pelagic larvae I have found such organs only in *Spio martinensis Type II* (fig. 27a).

Pigmentation

On the whole it can be said that two types of pigmentation occur in the treated larvae, viz. a structureless pigmentation dissolved in the cells, and a grainy type which appears either as melanophores or chromatophores, or as grains of melanin or other kinds of pigments in the epidermis cells. Pigmentation of the first-mentioned type is observed in almost all of the larvae. The grainy type is considerably more common in the subfamily *Spioninae*. Melanophores occur only in this subfamily.

The structureless pigmentation may be of varying colour. Here green, blue, orange, red of different kinds, etc. are observed. Especially prostomium, pharynx, and anus are richly provided with such pigment (pharynx and anus often have melanin as well).

There are several kinds of grainy pigment. Melanin with colours in black, brownish-black, brown, yellowish-brown, reddish-brown, etc. belongs within this group. This can either be bound to melanophores or chromatophores, or occur as small grains in the cells. The last-mentioned kind of melanin is found here and there in the larvae. It seems to be completely absent in *Laonice* and *Poecilochaetus*, but occurs more or less fully developed in the others with the exception of those which have melanophores. It is characteristic that the number of these melanin grains increases with age. For example, this pigmentation in *Nerine foliosa* is very faint in the younger stages (figs. 2a–e), but is most often vivid in older larvae (fig. 2g). In *Spio multioculata* such pigment is totally lacking in the young stages (fig. 20a), but prior to the metamorphosis it begins to appear along the dorsal side and laterally in the anterior segments (fig. 20b). The increasing distribution of the grainy pigment with increasing age is also noticeable regarding the yellow (reflected light) pigment, which will be discussed in the following.

The melanin is found bound to melanophores only in the subfamily *Spioninae*, where the majority of the species possess it. Only *Spio martinensis Type II*, *Spio theeli*, and *Spio multioculata* lack melanophores. The melanophores may be of two types: those with invariable form, and those which ramifications and a changeable form (regarding the variability

of form see *Polydora pulchra*, p. 132). Melanophores of the first mentioned type are found in *Pygospio*, certain *Spio* and *Microspio* species, and certain *Polydora* species. The last-mentioned type occurs exclusively in *Polydora*, but not in all species. In many of the larvae of this genus there is a melanophore of variable form between the median eyes on either side.

The grainy pigmentation which next to melanin has the widest distribution is composed of a pigment which is yellowish-green or yellowish-white in reflected light. In the microscope it appears black due to its opacity. It increases in distribution with age. This pigment type, which is otherwise very common among pelagic larvae of widely separated groups, is confined to the genera *Polydora*, *Spio*, *Microspio*, *Scolelepis*, and *Poecilochaetus* among the families treated. In the last mentioned it forms lateral chromatophores on the anterior side of the segments. It occurs in a similar manner also in *Polydora pulchra*. Otherwise these chromatophores may be placed in many ways. This pigment is observed diffusely scattered in the autumn larvae of *Polydora ciliata*.

A diffusely scattered, granular, bright red pigment is found along the dorsal side in *Prionospio steenstrupi*, and on the edge of the "umbrella" in *Disoma multisetosum*.

In summarizing it may be said that pigmentation is on the whole most vividly developed in the subfamily *Spioninae*, and in the genera *Scolelepis*, *Nerine*, and *Nerinides*.

Larval setae

There are numerous examples of pelagic organisms increasing their floating ability by the development of processes or bristles which increase their surface. The larval setae of the Spionids have been interpreted in the same manner. Other functions are, however, conceivable. Gravely (1909) assumed that these bristles, when extended, should serve as a protective device against smaller predaceous animals. For Wilson's (1928) conception of the significance of the bristles see page 161.

The larval setae are formed very early in the metatrochophora stage, and long before the adult bristles. The larva bears them thereafter during the entire pelagic life with few exceptions, foremost, *Poecilochaetus* (p. 139). In almost all the examined larvae the larval setae occur only dorsally in the parapodia. Robustly formed ventral larval setae occur only in *Laonice*, where they are of almost the same size as the dorsal ones (p. 25).

The larval setae are always longest in the first segment, and then occur in all segments with posteriorly decreasing length. An exception is the fifth segment in certain *Polydora* species, where larval setae are never developed (see for example fig. 35).

The larval setae vary in type in different species. As a rule they are

always set with fine serrations. These can either be evenly distributed around the entire seta, or set unilaterally or multilaterally. The vast majority have setae of the firstmentioned type. Robust examples are found in *Nerine cirratulus* and *Aonides paucibranchiata*. In other species the setae are thinner. In *Prionospio* and *Spiophanes* they are very thin. *Laonice* has very characteristic unilaterally serrated "*Chaetosphaera*"-setae (p. 25 and fig. 6 d).

Adult bristles

In all the examinated species bristles of the permanent type are formed already during the pelagic stage. The formation of these takes place at varying ages.

The adult bristles are with a few exceptions of the same type as in the adult stage. The modified bristles in segment 5 in the larva of *Polydora ciliata* lack, for example, partly a small lateral serration which is characteristic of these bristles in the adult. Söderström (1920) has demonstrated in *Nerine foliosa* that young individuals have hooded crochets which differ from those of the adult. In the first mentioned they are, namely, diserrated, but uniserrated in the later, an observation which I have been able to verify in cultures of this species (p. 15). There is a similar circumstance in *Spio martinensis*, where the larva and the recently metamorphosed worm has triserrated hooded crochets, and the older worm diserrated. Fauvel's (1927) report that *Spio filicornis* should have triserrated bristles when young and diserrated when older is due to confusion with *Spio martinensis*. Small individualities occur in bristles from different specimens and, also between e.g. hooded crochets from different segments of one and the same individual. Such variations are, nevertheless, rarely so great that there is any difficulty in identifying the bristles.

While the bristle in the larva differs insignificantly from that of the adult, there are naturally great differences in size and number per segment. Neither do adult bristles of certain type appear in the same segment in older and younger individuals. The equipment of ventral crochets provides a typical example. These are usually found very much more anteriorly in the young compared with adult individuals. On the other hand, I have never encountered the opposite condition. The following summary will illustrate this.

From the table it is seen that the crochets are developed from about segment 10 (7–16). In the *Polydora* species, *Microspio atlantica*, and *Pygospio elegans* the most anterior crochet-bearing segment in the larva is also the most anterior crochet-bearing in the adult. In other species the crochets are eliminated in a number of anterior segments. This elimination takes place continuously during the development, beginning with the first crochet-

Species	Ventral crochets from segm. no.		Size of adult worm	
	in larvae	in adults	segments	centimeters
Nerinides tridentata	13	15–16	60–70	1.6–2.0
Nerine foliosa	c. 10	58–60	200–250	6.0–16.0
Nerine cirratulus	c. 10	40	150–200	5.0–8.0
Nerine sp. I	?			
Nerine sp. II	15–16			
Laonice cirrata	14	40–50	160	9.0–12.0
Aonides oxycephala	8	32–35	100–200	5.0–10.0
Aonides paucibranchiata	9	36	54–80	1.8
Spiophanes bombyx	12–13	15	180	5.0–6.0
Spiophanes kröyeri	c. 13	c. 15		
Prionospio malmgreni	10	12–13	60	2.0–2.5
Prionospio steenstrupi	9	16–21	100	4.0–4.5
Prionospio cirrifera	10	15–18	83–87	3.0
Scolelepis ciliata	8	20–28	80–100	3.0–4.0
Scolelepis fuliginosa	8	30–45	100–150	5.0–6.0
Scolelepis Girardi	8	30–40	200–350	10.0–16.0
Spio filicornis	9	10	80–90	3.0
Spio multioculata ?	10	28–32		2.0–2.5
Spio theeli	11	17–22		
Spio martinenis Types I + II	11	13–15	85–90	
Microspio atlantica	9	9	32	0.85
Pygospio elegans	8	8	50–60	1.0–1.5
Polydora ciliata	7	7	60–180	2.0–3.0
Polydora ligni	7	7		
Polydora hermaphroditica	7	7	40–65	1.2–1.5
Polydora flava	7	7	100–150	2.0–4.5
Polydora coeca	7	7	70–130	2.0–4.0
Polydora caulleryi	7	7	40	0.8
Polydora antennata	8	8	65–100	2.0–3.0
Polydora pulchra	8	8	44	1.1

(The data concerning the size are taken from FAUVEL 1927)

bearing segment. There is a tendency that the larger the species becomes as adult the greater the number of anterior segments where the crochets are eliminated.

"Bacillary glands"

I do not intend to go into greater detail regarding the different epithelial glands which occur in these larvae, but will limit the discussion to one type which is very characteristic and is found in a large number of species. It is the spool-shaped type with longitudinally striated glandular contents

which has been called "bacillary glands" (JÄGERSTEN 1952). Such glands are usually found in the pygidium (especially abundant in, e.g., *Scolelepis*, *Prionospio*, *Spiophanes*, etc.), but they may also occur in the prostomium (e.g., *Pygospio elegans*, *Polydora flava*). In *Pygospio*, and some of the *Spio-Microspio* species such glands are found on the dorsal side, where they are often arranged in a characteristic pattern, and in the dorsal cirri (*Spio multioculata*). The glands are stained with iodine green, and probably produce a mucous secretion.

Systematic Value of Larval Morphology

In the arrangement of a natural system it is desirable that all age stages of the animals be taken into consideration. In the systematic treatment of many animal groups this has not been possible. This is true, among other groups, also of the polychaetes, where the larval development is known up to the present time in rough outlines only.

In this work I shall try to elucidate the systematic conditions within *Spionidae*, *Poecilochaetidae*, and *Disomidae* by means of the larval morphology. In such an undertaking a series of factors must be considered.

The larva exhibits characteristics of three main kinds and of varying value in the systematic treatment, viz.:

1. Specifically larval characteristics. With this are meant those which do not persist in any form in the adult animal. Some of these may be regarded as adaptations to a pelagic mode of life, viz., the larval ciliation and larval setae. Among these, however, must also be counted other characteristics as the "ciliated pit", larval eyes, and larval pigmentation.

2. Larval characteristics, which through transformation (metaplastic growth) are converted into adult features. Among these I count the larval forms of the prostomium, peristomium (including its lateral parts, vestibule, etc.), pygidium, etc.

3. Adult characteristics. Here are included those characteristics which without transformation grow to their adult form (orthoplastic growth), e.g. the parapodia, branchiae, and also the so-called adult bristles.

Naturally such a classification must be artificial, and transitional types between the groups exist. By way of example, certain nototrochs will remain relatively unaltered, but acquire a changed function.

In this connection it is naturally the properties under 1 and 2 which are of the greatest interest.

Characteristic of the different groups are not mutually independent, but inter-reaction occurs. This has already been observed by GRAVELY (1909). He says in part: "Characteristics of apparent systematic value in larvae

may be due to either of two distinct causes, which is necessary clearly to distinguish from one another on account of their different phylogenetic values. Either they may be due to inheritance by all members of the group whose larvae they characterise, from a common pelagic ancestor or from the pelagic larva, specially modified through the agency of natural selection, of some common but less remote creeping ancestor, or they may be due to some *correlation between adult and larval structures*" (my italics). As an example of such a correlation between adult and larval characteristics GRAVELY (op. cit.) names the larvae of *Telepsavus costarum* (*Chaetopteridae*) which had been described earlier by CLAPARÈDE and MECZNIKOW (1869). This larva has a very markedly reduced prostomium. The formation of a robust prototroch is therefore out of the question, and it has been completely reduced. This has, however, been compensated by the development of a very robust troch more posteriorly on the larval body. This is situated in a place which will be a boundary between two regions of the body in the adult animal. Such correlations between adult and larval characteristics are rare in the larvae of the families treated here. As an example, it may be mentioned that the fifth segment in certain *Polydora* species, i.e., the segment which bears the large modified bristles, lacks larval setae. The divergent ciliation in *Disoma multisetosum* (see p. 142) must be regarded as correlational phenomenon between characteristic group 1 and 2. In conjunction with the enormous enlargement of the peristomium during the pelagic stage the prototroch becomes very robust. On the other hand the gastrotrochs are weakly developed and will be completely discarded towards the end of the pelagic stage.

Larval Morphology and Developmental Type

It has long been known that the larval morphology in many marine animal groups is strongly dependant on the developmental type. Larvae with direct development tend to reduce a series of larval organs which are developed in pelagic larvae (cf. THORSON 1951). The polychaetes are no exception to this rule. SCHNEIDER (1913) established the great difference between the larva with a pelagic development and the one which developed without a pelagic stage in *Nereis dumerilii*. HÄCKER (1896) showed that polychaetes which spent part of their life under parental care had a so-called protrochophora stage, i.e. a stage where a broad ciliated area was formed around the peristomium instead of the narrow prototroch of the trochophore. SHEARER (1913) thought that the protrochophore type should be regarded as primitive. He showed that *Eunicidae* had pelagic larvae of this type. He believed that the trochophore was more specialized and thus

had developed from a protrochophoral larval type. SEGROVE (1941) agreed in principle with SHEARER's interpretion. He wrote: "The solution of the problem appears to me to lie in the egg. True trochosphaera larvae develop from comparatively small eggs, poorly supplied with yolk, whilst, on the other hand large yolky eggs give rise to larvae in which the typical trochosphaere features are more or less suppressed."

In the *Spionidae* there is no protrochophore stage. Independently of the developmental type the ciliation is formed largely after one and the same pattern. In species with wholly pelagic development and eggs very rich (e.g. *Aonides*) and poor in yolk (e.g. *Prionospio*), in species with brief parental care (e.g. *Polydora ciliata*) or prolonged parental care (e.g. *Pygospio elegans*) the prototroch, telotroch, gastrotrochs, and nototrochs (with a few exceptions) are developed. Irregularities or, more correctly, incomplete homodynamy in the location of the gastrotrochs is, of course, characteristic of brood-protecting species, but it occurs also in three species belonging to the genus *Scolelepis*, which have an entirely pelagic development.

The brood protection in *Spionidae* is, however, attended by certain reduction phenomena. The most remarkable of these is the reduction of the thickness of the egg membrane and the reduction of membrane vesicles. A tendency towards reduction of the vesicles is, however, observed in a genus without parental care, viz. *Prionospio*. In *Prionospio malmgreni* they are completely eliminated. A reduction of the "ciliated pit" in many of the brood-protecting species presumably must not be regarded as a direct consequence of the parental care. In several brood-protecting species this structure is very well developed. The larval setae may, however, be subject to reduction in the brood-protecting species. *Pygospio elegans* thus does not acquire these in direct development (SÖDERSTRÖM 1920); during parental care up to the 14–15-segment stage they may, however, develop.

On the whole it may be said that the developmental type in the treated families has a relatively slight significance for the morphology of the larvae.

Common Characteristics of the Larvae of the Treated Families and a Comparison with the Larvae of Closely Related Families

In a summary GRAVELY (1909) characterized the *Spionid* larva by its serrated larval setae which are always longest in the first segment, by the interparatrochs (with which he meant the noto- and gastrotrochs) which are inserted between a prototroch and a telotroch, and by its vestibule. This characterization is excellent. It applies, however, not only to *Spionidae*

but, as is evident from what has been said in the foregoing, also to *Poecilochaetus* and *Disoma*. There are, moreover, additional features which link these polychaete families together. The eggs in all of them (with the exception of the subfamily *Spioninae*) are of the same type, provided with a thick egg-membrane, and with the characteristic membrane vesicles. Furthermore, there is a "ciliated pit", except in certain *Polydora* species and *Pygospio elegans*.

Larval setae of the long serrated type are not entirely unique for the larvae of the treated families. They occur, e.g., also in *Sabellaria* (Wilson 1928) and *Owenidae* ("*Mitraria*"-larvae). The larval ciliation may be subjected to quite considerable reduction. This is especially true of the nototrochs, but also of the gastrotrochs which are, however, always found in some form in the treated larvae. The vestibule may vary in its formation. Nevertheless it must be said that the larval type is well separated from those of the closely related families.

The development in *Ariciidae* is well known from a series of studies (Eisig 1914, Okuda 1943, Horn and Bookhout 1950). In all the *Ariciid* species examined the eggs are laid in formed structures and have a thin egg-membrane. Gastrotrochs are found in two of the species, viz., *Haploscoloplos kerguelensis* and *Haploscoloplos bustoris*. Otherwise there are no great similarities with the treated larval type. The larval setae are not of the same type as in *Spionidae*, although as finely serrated, the neurotroch extends through a large number of segments, a "ciliated pit" is lacking, the vestibule seems simplified, etc.

The *Magelona* larva agrees in one respect with the treated larvae, viz., by having long larval setae. These are, however, not serrated in this larva. Otherwise the similarities are very slight. Larval ciliation is lacking, the mouth region deviates, a "ciliated pit" is lacking, etc. Its egg lacks membrane vesicles and has a thin egg-membrane (McIntosh 1878).

The *Chaetopterus* larva differs in all characteristics. It has a divergent shape, different ciliation, and lacks larval setae, etc.

Cirratulidae also have a strongly divergent larval development (Caullery and Mesnil 1898, Okuda 1946, Stephenson 1950).

It is of course, conceivable that additional families may possess the foregoing larval characteristics. The development in *Apistobranchidae* and *Paraonidae* is still unknown. Neither of these, however, has eggs of the thick-membraned type and membrane vesicles.

In this connection Häcker's (1896) "*Rostraria*" larva must be mentioned. It agrees in several important points with the treated larvae. It has, for instance, long larval setae. Regarding the ciliation it is apparent from Häcker's illustrations that gastrotrochs, nototrochs, and a telotroch are found. A prototroch seems to be missing. The "*Rostraria*" larva resembles

Fig. 56. "*Rostraria*"-larva (dorsal view).

the larva treated in this paper even in regard to the shape of body. On one occasion (July 1949) a "*Rostraria*" larva has been obtained in plankton from the Gullmar Fjord (fig. 56). Unfortunately it was in very poor condition when I examined it and this together with my inexperience at that time resulted in a very superficial study.

HÄCKER (op. cit.) proposed that the "*Rostraria*" larva should be referred to *Disomidae*. This proposal was based primarily on the fact that the dorsal cirri were lobate in one of the examined larvae. According to SAINT-JOSEPH there should be a certain systematic connection between *Disomidae* and *Amphinomidae*. The latter has furcal bristles in the adult stage, and HÄCKER considered this a substantiation of his assumption as the larvae have bristles of this type. In my opinion there are good reasons for classifying the larva in *Amphinomidae* or *Euphrosynidae*. EHLERS (1913) arrived at the same conclusion after having examined a South Atlantic "*Rostraria carunculata*". In any case the *Rostraria*-larva cannot be referred to *Disomidae* (see p. 140). I have previously pointed out that *Euphrosynidae* and *Amphinomidae* have eggs which agree to a certain extent with the thick-

membraned type of the treated families. If it could really be ascertained that the "*Rostraria*"-larva belonged to *Amphinomidae* or *Euphrosynidae*, this would give rise to very interesting systematic aspects.

Hofker (1930) described a larva which has several characteristics in common with the larval type characterized in the foregoing. It had a prototroch and a telotroch (the sketch is wanting in detail and therefore it is impossible to determine whether it had noto- and gastrotrochs), two pairs of black eyes of which the distal pair is larger, rather short and robust larval setae in all segments, and ventral crochets from segment 8 onwards. The form of the crochets was typical of *Streblospio dekhuyzeni*. For this reason Hofker referred the larva to this species.

Discussion of the Systematic Connection between *Spionidae* Sars, *Disomidae* Mesnil, and *Poecilochaetidae* n.fam.

Mesnil (1897) formed the family *Disomidae* of *Disoma multisetosum*, described by Oersted (1844), and *Poecilochaetus fulgoris*, described by Claparède (in Ehlers 1875). He believed that this family should have a position between *Spionidae* and *Chaetopteride*.

Allen (1904), who treated the anatomy of *Poecilochaetus serpens* in greater detail, found this family justified. He wanted, however, to give it a position closer to *Spionidae*. He called attention to the great similarities in the formation of the palpi and the type of egg. Eisig (1914) considered that *Spionidae*, *Disomidae*, *Apistobranchidae*, *Paraonidae*, and *Ariciidae* formed a natural group among the spiomorphic polychaetes. Söderström (1920) studied the similarities of the eggs of *Spionidae* and *Disomidae* and found, moreover, that the muscular cells in these two families were of a type which was not found in the closely related families. For these and other reasons he let *Disomidae* form a subfamily in *Spionidae*, which he called *Disominae*. In a work published in 1925 Mesnil maintained his earlier view of *Disomidae* as a family well separated from *Spionidae*.

It has been stated in an earlier chapter (p. 174) that there are also very great similarities in regard to the larval development in *Spionidae*, *Disoma*, and *Poecilochaetus*, and that these diverge distinctly in this respect from the closely related families. They should, therefore, in my opinion be regarded as constituting a well defined group among the spiomorphic polychaetes. On the other hand, I do not share Söderström's idea of combining them in one family. Such a family would have to high a degree of disparity in relation the other spiomorphic polychaete families. But neither can I find any justification for combining *Disoma* and *Poecilochaetus*

into one family. Such a family, i.e. MESNIL's *Disomidae*, is in its turn disparate in relation to *Spionidae*. The disparity within *Disomidae* has earlier been demonstrated by EISIG (1914) concerning the adult animals. He found the following similarities between *Disoma* and *Poecilochaetus:* "...die Teilung des Körpers in Regionen, die Palpen, die rostrad gerichteten Podien des erstens Segments, die flaschenförmigen Cirren, die starken notopodialen Haken des Hinterleibs (aber bei *P.* reihenförmig und nicht wie bei *D.* spiralig angeordnet) und endlich die fadenförmigen, nicht typischen Kiemen (anstatt auf der Bauchfläche wie bei *D.* stehen diese Kiemen bei *P.* vom 21. Segment an in je einem Paare an der Hinterfläche jedes Notopodiums und jedes Neuropodiums; ...". But he also found that *Poecilochaetus* differed from *Disoma* "durch den Besitz eines medianen Tentakels, durch das höchst eigentümliche, weil aus drei tentakelartigen Anhängen gebildete Nackenorgan, durch den Mangel blattförmiger Neuropodien mit serialen Papillen, durch den Besitz von Seitenorganen, durch seinen kurzen sphärischen, epithelialen Rüssel, durch gefiederte Borsten und endlich durch die zahlreichen epithelialen Papillen" and stated, "Das sind sehr tiefgreifende Unterschiede für zwei Gattungen ein und derselben Familie". If one studies the characteristics stated by EISIG it is found that a couple of them, which are common to the two genera, are also observed in *Spionidae* (the regional division of the body and the palpi). Two of the similarities are very slight, viz., in regard to the branchiae, and the notopodial crochets, whereas the difference are appreciable.

Turning to the larvae, as is evident from the previous summary of the external larval morphology, very great divergences are also encountered here in the formation of the prostomium and the peristomium (including the vestibule and lateral parts) and the prototroch. Each one of the two larvae deviates in its own manner from the Spionid larva. *Poecilochaetus* undoubtedly stands closest to *Spionidae*. The young larva agrees in most points with the Spionid larva. In the continued development profound differences arise, e.g., the tritentacled nuchal crest, early reduction of the lateral parts of the peristomium, etc.

I am therefore of the opinion that the new family *Poecilochaetidae* should be taken out of *Disomidae* Mesnil. The three families, *Spionidae*, *Disomidae*, and *Poecilochaetidae*, constitute, however, a well-defined group among the spiomorphic polychaetes.

Discussion of the Systematic Relations within *Spionidae* Sars

In his systematic treatment of the *Spionidae* Mesnil (1896) made use of mainly the external morphology of the animals. He divided *Spionidae* into

two large groups: I. Species which has an anteriorly more or less narrowing prostomium, and II. Species which has a pair of lateral prostomial prosses. For further division he employed the segmental occurrence of branchiae, the fusion of the anal cirri, the occurrence of dorsal crochets, and the presence or absence of anterior hairy bristles in crochet-bearing segments.

To Spionidae he also referred *Magelona* and *Hekaterobranchus* Buchanan (= *Streblospio* Webster). In one genealogy he placed *Spio* in a central position.

In contrast to Mesnil, whose system he strongly criticized, Söderström (1920) employed mainly the appearance of the sexual products and the internal morphology of the adult animals in setting up his system. Above all he stressed the differentiation of the atoquous and epitoquous nephridia. For further division he made use of the type of dorsal organs, the number of atoquous segments, etc. As has been mentioned, he classified *Disomidae* as a subfamily in *Spionidae*. He found that *Spio*, *Microspio*, *Pygospio*, and *Polydora* formed a group which was well separated from the other genera. In these the differences between the epitoquous and atoquous nephridia were very great. Furthermore, the epitoquous nephridia were formed in different manner in males and females. The male nephridia were complicated organs for the formation of spermatophores (at least in some species), and in the female the vents of the nephridia were drawn up towards the dorsomedian line. In the females there were also dorsal receptacula seminis. The eggs did not have a thick membrane and the sperms were provided with a long head. In the other genera he found eggs with a thickened membrane and sperms with a short head. These genera lacked dorsal receptacula seminis. With the exception of *Disominae* he divided these genera into two subfamilies, namely, *Nerininae* and *Laonicinae*. The former was characterized by the fact that there was a slight difference between the atoquous and epitoquous nephridia. Here he classified the genera: *Nerine* Johnston (= *Scolelepis* Blainville sensu Mesnil pro parte), *Colobranchus* Schmarda (= *Scolelepis* Blainville sensu Mesnil pro parte), *Scolecolepis* Blainville (= *Nerine* Johnston sensu Mesnil), and *Aonides* Claparède. The subfamily *Laonicinae* was characterized by greater difference between the atoquous and epitoquous nephridia. The epitoquous lacked an external vent and opened instead under the cuticle. Pockets for genital products were found in many species. From this comparison it is evident that Söderström's system is based largely on reproductive characteristics.

I shall now proceed to a comparative study of the morphology of the larvae, and study to what extent a system based on these findings agrees with Söderström's.

It has been ascertained earlier that the two groups into which the *Spionidae* can be divided, i.e., one with and one without brood protection,

correspond to SÖDERSTRÖM's two main groups, viz. (I) Species with thickened egg-membranes, and (II) Species with thin egg-membranes, where (I) has entirely pelagic development, and (II) passes a part of the development in formed structures. Furthermore, it is apparent from my summary that a series of characteristics distinguishes the larvae of these two groups.

Organ	SÖDERSTRÖM's Group (I) minus *Scolelepis*	*Scolelepis*	SÖDERSTRÖM's Group (II) (subfam. *Spioninae*)
Peristomium	Lateral parts as a rule well demarcated (exception *Prionospio*).	Lateral parts well demarcated.	Lateral parts never well demarcated.
Eyes . . .	Two pairs of simple eyes, red (one exception).	Three pairs of black eyes. Lateral = double.	Three pairs of black eyes. Lateral = double.
Palpi . . .	Attached far out on the lateral parts of the peristomium.	Attached far out on the lateral parts of the peristomium.	More medially attached.
Parapodia .	Differentiated late.	Differentiated early.	Differentiated early.
Nototrochs .	Weakly developed or completely lacking.	Weakly developed.	Usually well developed.
Gastrotrochs	Regularly in each segment caudad of the "ciliated pit".	Regularly in alternate segments caudad of the "ciliated pit" or irregularly (*S. girardi*).	Regularly in alternate segments caudad of the "ciliated pit" or irregularly (*Polydora*).

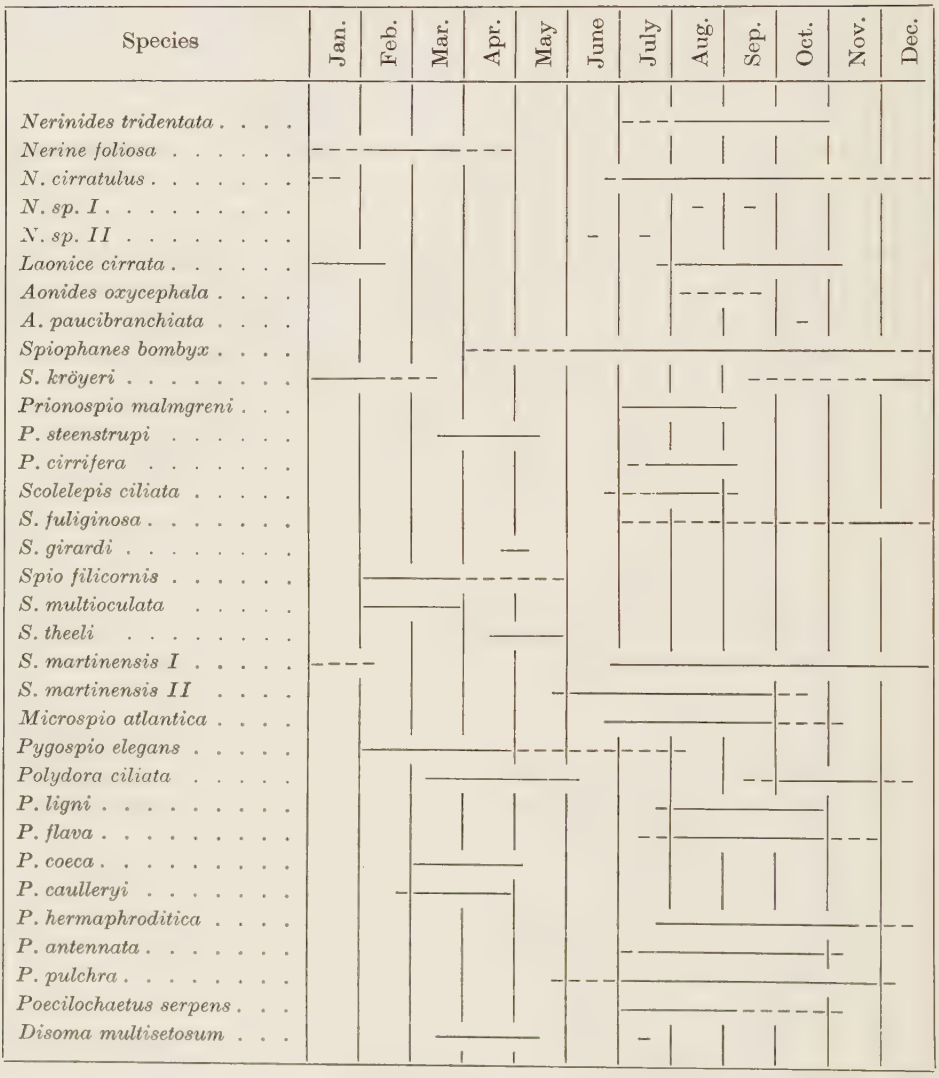
From the comparison it is seen that the *Spionidae* can be divided into three groups in regard to larval morphology. The first of these corresponds to SÖDERSTRÖM's Group (I) minus *Scolelepis*, the second comprises *Scolelepis*, and the third SÖDERSTRÖM's Group (II) (subfamily *Spioninae*). *Scolelepis* occupies an interresting intermediate position by having characteristics in common with both the other groups. Jointly with Group (I) it has the egg-type, formation of the lateral parts of the peristomium, the weakly developed nototrochs, and the point of attachment of the palpi: with Group (II) the number and colour of the eyes, and the arrangement of the gastrotrochs. It should, however, be placed closer to Group (I) than to Group (II). *Scolelepis* must, however, be removed from SÖDERSTRÖM's subfamily *Nerininae* in view of the morphology of the larvae. The larval morphology does not provide any information for a further division of Group (I) into the subfamilies *Laonicinae* and *Nerininae*. Within Group (I) only a number of genera can be distinguished with a more distinct demarcation of the lateral parts of the peristomium, viz., *Nerine*, *Nerinides*, and *Laonice*. This part of the peristomium become less pronounced in *Spiophanes bombyx*, *Spiophanes*

Kröyeri, and the *Prionospio* species in the order named. The younger *Aonides* larvae at any rate have relatively well demarcated lateral parts of the peristomium, and in this respect the genus is close to *Nerine*, *Nerinides*, and *Laonice*. *Prionospio*, which genus SÖDERSTRÖM regarded as being very close to *Laonice*, exhibits both in the egg-type (tendency towards reduction of the membrane vesicles) and in relatively far advanced reduction of the lateral parts of the peristomium a considerably less primitive developmental type.

Group (II) (subfamily *Spioninae*) is relatively uniform in regard to larval morphology. The egg has a thin egg-membrane, the lateral parts of the peristomium are not very conspicuous and weakly demarcated from the prostomium, the nototrochs become well developed, etc. Regarding the location of the gastrotrochs the subfamily can, however, be divided into two groups. In the one the gastrotrochs occur regularly in alternate segments caudad of a "ciliated pit", and in the other, where a "ciliated pit" is generally lacking, the gastrotrochs appear with a certain irregularity (within the genus as well as within one and the same species in certain cases). In the former group I classify the genera *Spio-Microspio*, and in the latter *Pygospio* and *Polydora*. The last-mentioned group is naturally to be regarded as the most modified within the *Spionidae*.

III. BIOLOGICAL PART

Occurrence of the Pelagic Larva in Plankton



The above table is based on all observations up to and including 1953. It is therefore a compilation of observations from several years.

From the foregoing it is evident that no species occurs in plankton throughout the year, but that all are more or less seasonal. Many have been obtained only during a brief period each year. This is true of, e.g., *Scolelepis girardi*, the two *Aonides* species, *Spio theeli*, *Polydora coeca*, *Polydora caulleryi*, etc. Others are found during a large part of the year. Extreme illustrations of this are *Spiophanes bombyx* and *Spio martinensis Type I*. It seems as if the spring-spawning species generally had a shorter season than those which spawn in the late summer and autumn.

For two years I have been able to make a continuous study of the plankton; thus during 1951 and 1952 I have not found any greater deviations in the onset and duration of the seasons. On the other hand, the number of individuals appears to be widely variable. During the summer of 1948 *Spiophanes bombyx* larvae appeared in much greater numbers than I have ever encountered since. During the autumn and winter of 1951 *Scolelepis fuliginosa* was almost completely absent. From December 10 to 20, 1948, however, it was exceedingly plentiful. Unfortunately I have not had an opportunity of making a quantitative analysis.

The number of species occurring in plankton at the same time is found to exhibit two maxima and two minima. The first maximum, which is of brief duration, occurs in March and April, and the second, which has a longer duration and is more pronounced, occurs during the period July to October.

Midwinter plankton is characterized by few species, and consists largely of a decimated summer–autumn plankton. Two species are, however, characteristic of this period, viz. *Nerine foliosa* and *Spiophanes kröyeri*. Their young stages are then obtained in abundance. Larger specimens of the first-mentioned species may be obtained until the beginning of April. Occasional specimens may be encountered as early as September. They are, however, not abundant until December. Of the late summer and autumn forms which are also encountered during the winter *Laonice cirrata* and *Spio martinensis Type I* may be mentioned. In February the number of species increases. The dominating ones are *Spio multioculata?*, *Spio filicornis*, and to some extent *Pygospio elegans*. At the end of March the number of species is further increased in conjunction with a more pronounced development of phytoplankton. The number of species culminates thereafter in April. The dominating ones are now *Polydora caulleryi*, *Prionospio steenstrupi*, and *Disoma multisetosum* in the order named, whereas the *Spio* larvae decrease in number. Of other species which appear in relatively large numbers *Polydora coeca* and *Spio theeli* may be mentioned. At the beginning of May the number of species begins to decrease. At this time *Polydora ciliata* predominates. Rare specimens of this species are obtained already in March, and as late as in June. In the latter month the

number of *Spionid* larvae is very small. Occasional individuals of the species which attain their maximum during the late summer and autumn now begin to appear. Such species are *Spiophanes bombyx* and *Polydora pulchra*. During July both the number of species and the number of individuals increase. The autumn maximum occurs and lasts for four to five months with a culmination in September–October. This is characterized at first by *Poecilochaetus serpens*, *Prionospio malmgreni*, *P. cirrifera*, *Polydora pulchra*, and to some extent *Scolelepis ciliata*. Later the number of *Spio martinensis* larvae of both types and *Polydora* species increases. Other important constituents are *Nerine cirratulus* and *Laonice cirrata*, which at times may occur in very great numbers, and to some extent *Nerinides tridentata*. During November the number of species gradually decreases, and the relatively scarceness in species of winter sets in.

The treated larvae have in the vast majority of cases a long pelagic life. Such larvae may with regard to their origin be divided into two categories, viz., allogenous and endogenous (Aurivillius 1898). For the former category of larvae at least four origins are conceivable. With the "Baltic Stream" coming from the south larvae from Öre Sound and the Baltic Sea are carried here. This takes place mainly during the spring and early summer. It is also conceivable that larvae are brought here from the north with the so-called "Water of the Northern Banks" (Gislén 1930) which generally runs as an undercurrent during the midwinter and early spring, and from the south with another undercurrent, the so-called "Water of the Southern Banks" (Gislén 1930) which comes in during the late summer and autumn. Finally, it is conceivable that larvae are carried by the so-called "34-water" (Gislén 1930), which lies as a deep layer in the Gullmar Fjord and is changed only periodically. Presumably a closer study of these conditions for which I have not had an opportunity would yield interesting results.

With so low a current-velocity as $\frac{1}{2}$ knot a larva with a pelagic development of one month, which must be regarded as normal for many species, is borne by the currents about 670 km. It is thus conceivable that incoming water carries *Spionid* larvae from distant regions. From this it is evident that conclusions cannot be drawn regarding the spawning in the area of a particular species simply on the basis of the occurrence of its larva in plankton. Neither can it be said with any absolute certainty that larvae which occur in plankton are found as adults in the area. As far as I know *Spio theeli* and *Spio multioculata* have never been encountered as adults here. They occur, however, every year as larvae. It is, moreover, probable that they will be obtained in a careful inventory of the fauna of the fjord. I have, namely, been successful in getting these larvae to metamorphose in bottom substratum from the fjord. It is likely that metamorphosis takes

place more readily on a suitable bottom substratum in nature than under laboratory conditions.

Course of Metamorphosis

The metamorphosis of the treated larvae is like that of many other pelagic larvae dependent on the nature of the bottom substratum (see compilations of THORSON 1946 and WILSON 1952). Substratum from the locality where the adult worm is found has a stronger inducing effect on the metamorphosis than others.

If a larva does not come into contact with such a bottom substratum it can prolong the pelagic stage. This ability is very great in certain species. I have found, e.g., that *Polydora ciliata* larvae can postpone metamorphosis up to one month, and that their ability of reacting to the right substratum is not thereby noticeably changed.

Spio martinensis Type I has been especially studied with regard to the course of metamorphosis.

When the larva which is ready to metamorphose comes into contact with a substratum intended to induce metamorphosis or, more correctly expressed, with water which is in contact with such a substratum it reacts first by sinking down to the surface of the substratum. It behaves more or less if a narcotic had been added to the water. It lies on the surface of the substratum either motionless or with a rapidly vibrating body. This period is of very varying length, from a second or two up to several minutes. Suddenly, however, it begins to crawl sinuously over the surface, and attempts now and then to burrow down with the prostomium first. Frequently this is accomplished, but in other cases the digging is discontinued, and the larva lies motionless for a few minutes, whereupon the digging is resumed. Such digging attempts may alternate with long periods of inactivity. It often happens that the larva swims away from the substratum for a few seconds or minutes, and then returns to resume the digging attempts. I am under the impression that the period which elapses between the larva's first reaction to the substratum and the final digging down is appreciably shorter in larger larvae than in smaller. The youngest larvae which are not ready to metamorphose do not react at all to the substratum. Systematic investigations on this point are, however, still to be carried out.

In conjunction with the larva's beginning to crawl over the surface of the substratum and attempting to dig down, the palpi are directed forward-upward. They have earlier lain pressed against the larval body obliquely downward-backward. The larval setae are usually lost in the actual pene-

tration into the substratum. In this connection the body extends in a longitudinal direction and is also flattened out somewhat on the sides. The parapodia appear through the extension as more demarcated from the body. The larval trochs are not immediately discarded. Examination of a larva about five minutes after penetration into the substratum reveals that they are still in motion. After about 20 minutes the trochs begin to undergo reduction, especially the gastrotrochs, and they no longer beat so actively. The prostomium has about the same appearance as in the larva (fig. 57 a), and the ventral lip has still not shown any tendency of being drawn forward. The notopodial cirri are more dorsally directed in the pelagic larva. About one hour after the metamorphosis the prototroch, gastrotrochs, and telotroch have been shed. The "ciliated pit", however, is still unchanged. The prostomium has undergone an extension. The ventral lip and the peristomium still have the same appearance as in the larva. After six hours the "ciliated pit" is reduced to a shallow groove without ciliation and thus the larval ciliation has entirely disappeared (fig. 57 b). The prostomium has been extended somewhat further. The lateral lips have to some extent begun to be drawn in under the ventral lip. The lateral parts of the peristomium have not yet undergone any noticeable alteration. The dorsal cirri are very clearly directed upward.

After this the transformation proceeds considerably more slowly. Rests of the larval pigmentation, for instances, are still found after two months, when the sexual products begin to be developed.

The processes of metamorphosis and transformation take place in essentially the same manner in all the *Spionids* studied. Larval features often persist for a long time during the development. This is true above all of the eyes, the pigmentation, and the location of the adult bristles (see p. 170).

Polydora ciliata, *P. flava*, and *P. coeca* deviate somewhat from the behaviour on contact with the substratum, described in the foregoing, by lacking a period of inactivity. As soon as they are ready to metamorphose they react by crawling at the contact with a suitable substratum (see further p. 104).

Disoma multisetosum corresponds in regard to the metamorphosis to the Spionids except for the fact that it sheds its gastrotrochs already during the pelagic stage.

Poecilochaetus serpens, on the other hand, has a metamorphosis of another type (see p. 137). In this species the entire larval ciliation is lost already during the pelagic stage. This species, moreover, also reacts strongly on contact with the bottom substratum according to the course previously described.

From a morphologic point of view the course of metamorphosis thus

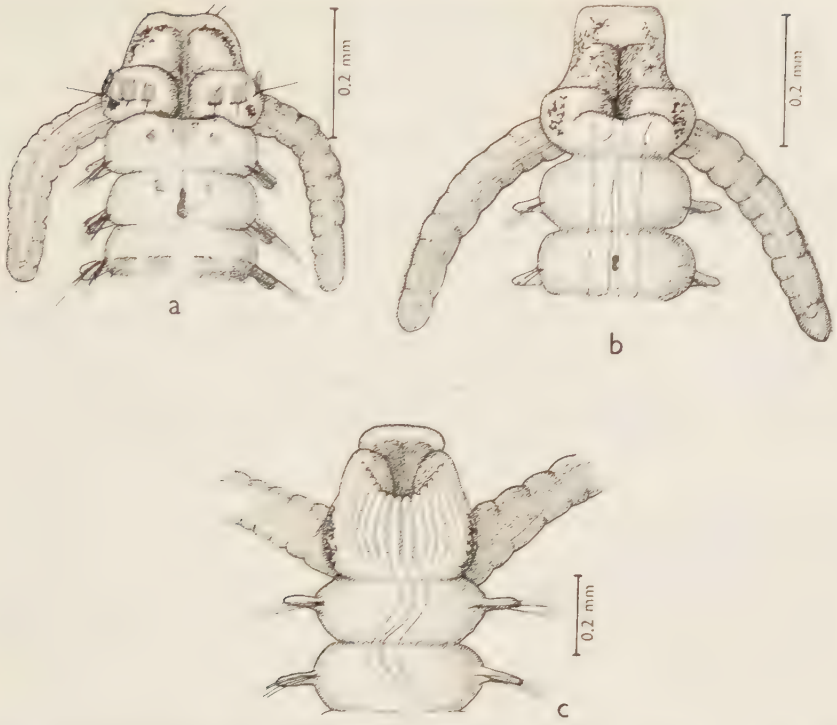


Fig. 57. The development of the mouth region of *Spio martinensis* Mesnil. Ventral views of the foreparts in different stages. a) Pelagic larva with 19 segments. b) Young bottom stage with 18 segments 6 hours after the beginning of benthic life. c) Young bottom stage with 31 segments 16 days after the beginning of benthic life.

varies considerably in different species. I have found it practical to define metamorphosis of these larvae as the process by which the larva irreversibly passes over into a benthonic life.

SUMMARY

1. The investigations have been carried out at the Gullmar Fjord on the west coast of Sweden.

2. The greater part of the examined larvae have been obtained from plankton. They were caught in plankton nets of different construction, fitted with filter cloth or varying coarseness. Vertical nettings have been carried out, and the number of individuals of different species has been counted in order to get an idea of the relative frequency during different days and seasons.

3. A number of experiments have been carried out with rearing from the egg to the adult stage.

4. Larvae and young benthonic stages have been figured from living specimens.

5. The larvae have been reared in small culture-dishes until their metamorphosis was obtained. The young benthonic stages were allowed to live until identification of the species was possible.

6. The pelagic larvae of *Nerine cirratulus*, *N. foliosa*, *Nerinides tridentata*, and two heretofore unidentified *Nerine* larvae are described.

7. The pelagic larva of *Laonice cirrata* is described. It is shown that the *Laonice* larva is identical with HÄCKER's (1896) "*Chaetosphaera*" larva.

8. The pelagic larvae of *Aonides paucibranchiata* and *Aonides oxycephala* as well as the young benthonic stage of the latter are described. The larvae have a developmental type which differs from that of the other Spionid larvae by their abundance of yolk.

9. The pelagic larvae and the young benthonic stages of *Spiophanes bombyx* and *Spiophanes kröyeri* are described.

10. The pelagic larvae and the young bottom stages of *Prionospio steenstrupi*, *Prionospio cirrifera*, and *Prionospio malmgreni* are described. In *Prionospio malmgreni* it has been possible to follow the entire development from the egg to the adult stage.

11. The pelagic larvae and the young benthonic stages of *Scolelepis ciliata* and *Scolelepis girardi* are described. A comparison is made between the larvae of the two closely related species *S. fuliginosa* and *S. ciliata*.

12. The justification in separating *Spio* and *Microspio* into two different genera is discussed. The author does not consider that SÖDERSTRÖM's (1920) basis for distinction is adequate. Further investigations must, however, be carried out before a definite conclusion can be reached on this point.

13. The pelagic larvae and the young benthonic stages of *Spio filicornis*, *Spio multioculata*, *Spio theeli*, *Microspio atlantica*, and two different larval types of *Spio martinensis* are described.

14. It is shown that the fusion of *Spio martinensis* and *Spio filicornis* into one species, as proposed by SÖDERSTRÖM (1920), cannot be upheld. It is discussed whether or not *Spio martinensis* should be divided into two species. These would be distinguished from each other through differences in regard to reproduction.

15. The development of *Pygospio elegans* is described. It is demonstrated that this species has a brood protection which varies in duration according to season. A relatively short period of parental care and a long pelagic stage occur in the late winter-early spring. During the summer the period of parental care is prolonged, and the pelagic stage is gradually shortened.

Contrary to what has been assumed of late it has been found that this species has larvae of only one morphologic type.

16. The pelagic larvae and the young benthonic stages of *Polydora ligni*, *Polydora flava*, *Polydora caulleryi*, *Polydora coeca*, and the new species *Polydora hermaphroditica* are described. From *Polydora* (*Carazzia*) *antennata* the variety *pulchra* is removed as a separate species on the basis of the relatively great differences in regard to the larvae. The pelagic larvae and the young benthonic stages of these species are described. A peculiar type of hermaphroditism combined with neoteny has been observed in *P. hermaphroditica*. A comparison is made between the pelagic larvae of *P. ligni* and *P. ciliata*. In *P. ligni*, *P. ciliata*, and *P. hermaphroditica* a hitherto undescribed gland has been observed in connection with the modified bristles in segment 5. This gland is assumed to be of importance for the larva when it bores its first tube. It may produce an acidic secretion which dissolves the lime, facilitating thereby the work in boring.

17. Pelagic stages of *Poecilochaetus serpens* are described. It could be ascertained that the pelagic life of this species is divisible into two phases. During the first a ciliation and larval setae are found, during the second these organs are lost. The phases are called the metatrochophore stage and the nectosoma stage.

18. The pelagic larva and the young benthonic stage of *Disoma multisetosum* are described.

19. Sexual products, type of reproduction, and pelagic larvae of the examined species are compared.

20. According to the type of reproduction the species of the area of investigation may be divided into two main groups:

I. Species with entirely pelagic development,

II. Species where part of the development takes place in formed structures.

To the former group belong the genera: *Nerinides*, *Nerine*, *Aonides*, *Laonice*, *Spiophanes*, *Prionospio*, *Scolelepis*, *Poecilochaetus*, and *Disoma;* to the latter the genera *Spio*, *Microspio*, *Pygospio*, and *Polydora*.

21. In regard to the manner of nourishment of the larvae the entirely pelagic larvae may be divided into lecithotrophic and planktotrophic. Only the larvae of the *Aonides* species are lecithotrophic.

22. Among the species which lay their eggs in formed structures the vast majority exhibit brood protection. In *Spio filicornis* and *Spio martinensis*, on the contrary, the formed structures are deserted by the mother.

23. The pelagic stage of species with brood protection may be extremely curtailed or totally lacking.

24. It has been ascertained that eggs with a thick egg-membrane and characteristic vesicles penetrating into the plasm, which are caused by

specialization in the membrane, are characteristic of the genera *Nerinides*, *Nerine*, *Aonides*, *Laonice*, *Spiophanes*, *Prionospio*, *Scolelepis*, *Poecilochaetus*, and *Disoma*. It is possible that similar eggs occur also in the polychaete families *Euphrosynidae* and *Amphinomidae*. A theory is advanced of the function of the mentioned vesicles in fertilization as volume-regulating organs. Eggs of a simpler type occur in the genera *Spio*, *Microspio*, *Pygospio*, and *Polydora*.

25. Also in regard to the appearance of the sperms the generic groups enumerated in the foregoing differ from each other by the specialization of the sperms for an internal fertilization in the latter group.

26. It is shown that the larva of *Disoma multisetosum* has a prostomium which differs from that of the larvae of the other genera by its higher degree of coalescence with the peristomium.

27. In *Poecilochaetus* the prostomium of young larvae agrees with that of the Spionids. In older stages, however, the larva develops a nuchal crest with a divergent form.

28. Two pairs of simple eye spots (red with one exception) are found in species belonging to the genera *Nerine*, *Nerinides*, *Aonides*, *Laonice*, *Spiophanes*, *Prionospio*, *Poecilochaetus*, and *Disoma*. In the other genera there are three pairs of eye spots, all of which are black. The most distal pair consists of so-called double eye spots.

29. The lateral parts of the peristomium in the genera *Nerinides*, *Nerine*, *Laonice*, *Scolelepis*, and to some extent *Aonides* and *Spiophanes* are well developed and clearly demarcated. *Disoma* deviates from the others in having a far-advanced fusion of prostomium and peristomium. In the others the lateral parts of the peristomium are relatively weakly developed and not well demarcated from the prostomium. It is shown that during the later development the lateral parts of the peristomium pass over into the base of the palpi. The organization of the vestibule is discussed and it is shown that a ridge in the vestibular tegmen in *Nerine*, *Nerinides*, and *Poecilochaetus* is more strongly developed than in the other genera and that it grows into anteriorly directed, robust processes.

30. In all the treated species the palpi appear already in the pelagic stage. In *Nerine*, *Nerinides*, *Laonice*, and *Aonides* they remain relatively insignificant during this period. In these genera as well as *Scolelepis* and *Spiophanes* they are attached far out on the lateral parts of the peristomium, in the others more medially. In *Disoma* and *Poecilochaetus* they are of different lengths.

31. The segments are formed gradually. The differentiation of the parapodia takes place earlier in certain species belonging to the genera *Spio*, *Microspio*, *Pygospio*, and *Polydora* than in the others. Branchiae are never formed in a segment which is not definitely branchial. The first-developed

pair can, however, be formed one segment posterior to the one which will become the first definitely branchial segment.

32. Two kinds of ciliation occur. One is bound to prolonged cells and forms distinct rows, the other is scattered over larger surfaces. Moreover, there are so-called "sensory cilia", which may appear separately or interspersed among cilia of the other types.

33. The prototroch is shaped as two rings of ciliated cells of which the anterior is reduced. In *Nerinides tridentata* and *Disoma multisetosum* the prototroch remains biserial during the entire pelagic life.

34. Nototrochs are as a rule found in *Spionidae* (exceptions: certain species of *Nerinae* and *Nerinides*), but are lacking in *Disoma* and *Poecilochaetus*. They become best developed in *Spio*, *Microspio*, *Pygospio*, and *Polydora*. In some of these they are composed already in the larva of two rows of ciliated cells. They persist in the adult stage in the branchial segments.

35. Gastrotrochs occur in all species. In all genera except *Scolelepis*, *Spio*, *Microspio*, *Pygospio*, and *Polydora* they occur in all segments from the third or fourth onwards. In the enumerated genera they occur either regularly in alternate segments from the third onwards (*Spio*, *Microspio*) or irregularly.

36. The telotroch is uniserial in all pelagic stages, and occurs in all genera like the prototroch.

37. Certain cells of the nototrochs are differentiated to so-called "grasping cilia" for the purpose of holding together the larval setae while swimming. They appear to be best developed in the genera enumerated in paragraph 35.

38. The neurotroch, which in type differs from the other trochs, is a short ventromedial ciliation which never extends more caudad than through segment 2. It may be lacking (e.g., certain *Polydora* species).

39. The neurotroch ends as a rule in a ciliated cavity ("ciliated pit"). This structure is situated in segments 1, 2, or 3. It is unique for, and characteristic of the treated species. On either side of this structure there occurs in certain species (*Nerine*, *Scolelepis*, *Laonice*) a pair of ciliated elevations, which are reduced in conjunction with the metamorphosis like the rest of the "ciliated pit" complex. The "ciliated pit" usually constitutes the common outlet for two systems of mucous glands. The anterior system consists of long epithelial tubes, which through a common, median, ciliated passage open into the anterior part of the "ciliated pit". Unicellular mucous glands open into the posterior part. In *Disoma* presumably glands are totally lacking. In the other species the number of anterior glandular tubes may be reduced and/or the posterior unicellular mucous glands may be totally lacking. In *Prionospio malmgreni* the "ciliated pit" is formed rela-

tively late in the 2-segment stage. A theory is advanced that the "ciliated pit" is a palingenetic organ without greater biological significance for the larva. The similarities between the "ciliated pit" complex and the foot glands of the prosobranchs have been pointed out.

40. Nuchal organs are found in all the examined larva with two exceptions (*Disoma multisetosum* and *Laonice cirrata*). They are formed on either side of the nuchal crest and are grooved-shape (longitudinal or transversal) or oval. In *Poecilochaetus serpens*, which has groove-shaped nuchal organs as a younger larva, they undergo a very marked development before the larva passes over into a benthonic life. In the genera *Spio*, *Microspio* and *Scolelepis* the nuchal organs, after at first having been parallel, acquire after the metamorphosis a very characteristic horseshoe shape.

41. The dorsal organs are developed relatively late only. Such have, however, been observed in one pelagic larva (*Spio martinensis* Type II).

42. The pigmentation in the described larvae is of two main types, namely (I) structured, and (II) structureless. Of the former occur above all melanin and a yellowish white pigment. The latter may comprize a series of different colours. The structureless pigment, and to a certain extent the melanin are most markedly developed in prostomium, pharynx, and anus.

43. The larval setae are formed earliest and attain their greatest length in the first setiger. All larval setae of the examined species are beset with serrations of varying coarseness. The form and coarseness of the bristles varies greatly. The appearance of the larval setae seems to have little systematic significance.

44. Bristles of the adult type are formed already in the larva. They have, with a few exceptions, the same appearance as the definitely permanent bristles. Ventral crochets are found most often more anteriorly in the body of the larva than of the adult. These anterior crochets are successively lost. There is a tendency that the larger the species becomes as adult the greater the number of anterior segments which will shed their crochets.

45. So-called "bacillary glands" occur in the epithelium in many of the described larvae.

46. On the basis of the morphologic character of the larva three divisions can be distinguished: 1. Specific larval characteristics. 2. Larval characteristics which are transformed (metaplastic growth) into adult ones. 3. Adult characteristics (growth without transformation).

In a system based on the larval morphology groups 1 and 2 are of the greatest interest.

47. The different groups of characteristics are not wholly independent of each other.

48. The type of development has been declared by a series of investiga-

tors to have significance for the larval morphology. This seems to be the case to a lesser degree in the treated larvae. Development through brood protection is attended by reduction of the thickness of the egg-membrane and elimination of the "membrane vesicles".

49. The development of the three families treated agrees in essential points.

1. The egg, with some exceptions (see the foregoing), is a characteristic type with a thick egg-membrane and membrane vesicles.

The larvae have:

2. Long, serrated, larval setae, which are longest in the first setiger.
3. Noto- and gastrotrochs inserted between the proto- and telotroch.
4. A vestibule of characteristic type.
5. A short neurotroch, which in segments 1–3 passes over into a "ciliated pit".

In the above characteristics these larvae differ from all other known larvae. It is possible that additional families will be placed in close connection to this group. The "*Rostraria*" larva shows much in common with the described larvae. Probably also *Streblospio* should be classified here, provided that a larva described by HÖFKER (1930) is correctly identified.

50. In view of the similarities in development *Spionidae*, *Disomidae*, and *Poecilochaetidae* ought to be regarded as constituting a well-defined group among the spiomorphic polychaetes. On account of the differences which are encountered within this group it is, however, not appropriate that they should be united in one family. The larvae of *Disoma* and *Poecilochaetus* diverge from that of *Spionidae*, each in its own way. Since the differences between the larvae of *Disoma* and *Poecilochaetus* are relatively great (above all in regard to the development of the head region), *Poecilochaetus* should be removed from the family *Disomidae* in order to form the new family *Poecilochaetidae*. The great differences between the adult animals also support this measure.

51. In regard to the larval morphology *Spionidae* may be divided into three groups:

1. Genera *Nerine*, *Nerinides*, *Aonides*, *Laonice*, *Spiophanes*, and *Prionospio*.
2. Genus *Scolelepis*.
3. Genera *Spio*, *Microspio*, *Pygospio*, and *Polydora*.

Group 2 occupies an interesting intermediate position by having characteristics in common with both groups 1 and 3. Within these groups no division on the basis of larval morphology can be made corresponding to SÖDERSTRÖM's (1920) classification into subfamilies.

52. A compilation of the occurrence of the different species in plankton is presented. They are all seasonal, and occur during periods of varying

length. Some species are encountered during two seasons every year. Regarding the number of species appearing simultaneously there are two maxima and two minima in a year. A spring maximum occurs during March–April, and an autumn maximum during July–October. The spring-spawning species are generally found during a shorter period than the autumn-spawning.

53. Since the larvae have, in most cases, a long pelagic life, conclusions cannot be drawn regarding the spawning of a particular species in the area of investigation simply on the basis of its occurrence in plankton, as the larvae may have been carried by currents from distant regions. Nor can for the same reasons any conclusions be drawn regarding the occurrence of a species in the area from the appearance of its larva in plankton.

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